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Hardwood Understory Depletes Soil Water In Pine Stands

BY
ROBERT ZAHNER

HARDWOOD UNDERSTORIES are common on most pineland in the Midsouth. As summer rainfall is often deficient in this area, it is probable that understories compete strongly with overstory pine for stored soil water. That portion of soil water used by understory hardwoods was recently measured in southern Arkansas. The study compared depletion trends during the growing season for well-stocked pine forests with and without understories. Also studied was the effect on moisture of partially controlling the hardwoods with prescribed burns.

Stone (1952) summarizes modern views that evapo-transpiration may be independent of the specific character of plant cover, and thus independent of understory. He suggests that this is true as long as soil moisture is plentiful, but that after the soil has dried somewhat, water loss is probably greatest where roots most fully occupy the soil.

On well-drained uplands in the southern Appalachians, Johnson and Kovner (1956) showed that the understory does have a significant effect on forest water use. A hardwood watershed with the understory removed yielded an annual average of 2 acre-inches of water more than a similar hardwood watershed on which the understory was left undisturbed. The difference was attributed to a 6-percent decrease in actual evapo-transpiration as a result of understory treatment.

Discussing soil-water depletion on watersheds, Kramer (1952) emphasizes the importance of the transpiring effectiveness of the crown canopy and the distribution of roots in the soil. His conclusions suggest that the leaf surface and root competition of an understory could remove considerable water from pine stands during periods of hot, dry weather.

The Study

Study areas. Two even-aged 50-year-old stands of loblolly-shortleaf pine (*Pinus taeda* L. and *P. echinata* Mill.) in Ashley County, Arkansas, were selected for study. Four quarter-acre plots were established in stand I in 1951, and six in stand II in 1954. Pine stocking on all plots within each stand was made uniform as to number and size of stems and basal area. Understory hardwoods, uniformly well developed on all plots, were chemically treated on two plots in each stand, so that all rootstocks were killed and eradication was complete (Fig. 1, *left*). The two extra plots in stand II were prescribed-burned in the spring of 1954 and again in the summer of 1955.

Two growing seasons were allowed for the residual stands to adjust crowns and roots to the original treatments. By 1953 for stand I and by 1956 for stand II, pine stocking was good on all plots, averaging 115 stems per acre, with average diameters of 12.5 inches and total basal areas of about 95 square feet.

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On the untreated plots, understory stems numbered up to 20,000 per acre, ranging in size from small shrubs to trees 20 or 25 feet tall (Fig. 1, *right*). The most common species were sweetgum (*Liquidambar styraciflua*), blackgum (*Nyssa sylvatica*), southern red oak (*Quercus falcata*), dogwood (*Cornus* sp.), persimmon (*Diosporus* sp.), haw(*Craetaegus* sp.), sumac (*Rhus* sp.), elm (*Ulmus* sp.), red maple (*Acer rubrum*), mulberry (*Morus* sp.), Hercules club (*Aralia spinosa*), and miscellaneous oaks (*Quercus* spp.) and hickories (*Carya* spp.). On the burned plots, most hardwood stems less than 3 inches in diameter at ground level had been killed back to the roots by the two fires, but sprouting was vigorous during 1956.

Site index for loblolly pine on the two areas was between 85 and 90 feet at age 50. The stands are on upland sites with a permanent water table at about 30 feet, far below the root zone. Both soils were classified as Lexington silt loam. This soil type is characterized by a dark grey silt loam surface soil which grades into a mottled yellow-grey silt loam subsoil at about 12 inches. Surface and internal drainage are imperfect. Physical soil properties are remarkably uniform among all plots, changing only gradually from the surface to a depth of 60 inches; average bulk density increases from 1.48 to 1.55, wilting point from 5 to 8 percent by weight, and field capacity (60 cm. tension) ranges from 22 to 25 percent by weight. Total available soil water storage in the surface 4 feet was calculated to be about 13 inches.

Sampling methods. Soil moisture was sampled periodically under treated and untreated plots from May through September during each year of the study. Stand I provided the data during 1953, 1954, and 1955, and stand II during 1956. Moisture was determined gravimetrically from samples obtained with a hammer-driven tube sampler as described by Olson and Hoover

FIGURE 1. *Left: Study area with hardwood understory removed. Right: With understory in place.*

(1954); then all data were converted to inches of available water.

The field procedure was altered from year to year in an attempt to obtain adequate soil moisture information with a minimum of sampling. Sampling intervals and intensities, and soil depths sampled, are consistent for all plots within any one year but may introduce variation in comparisions among years.

In 1953 and 1954, 50 by 50-foot subplots were located in the quarter-acre plots in stand I. At 2-week intervals, four sampling points were randomly selected in each subplot and soil samples taken from each at four depths down to 60 inches. Depths sampled in1953 were 0-6, 6-12, 20-26, and 42-48 inches. In 1954 the 6-12, 20-26, 36-42, and 54-60 inch depths were sampled.

In 1955 a more extensive method was used. Circular fifth-acre subplots were established in the centers of treated and untreated plots in stand I. Once each month ten sampling points were randomly selected in each fifth-acre (by a method proposed by Gaiser, 1951), and soil samples taken from each point at three depths, 6–12, 20-26, and 36-42 inches.

In 1956, the circular fifth-acre subplots were again used, this time located in the centers of all plots in stand II. At 3-week intervals, eight sampling points were established in each subplot, and three depths were sampled, 0–6, 12-18, 30-36 inches.

On each sampling date, replications within a depth were averaged by treatments. Then soil-moisture data from the individual depths were combined to give the total moisture content of the upper 48 inches of soil. This layer has previously been shown to be of greatest importance in water depletion from forests in southern Arkansas on similar silt loam soils (Zahner, 1955).

Rainfall. During each year of the study, spring rainfall was sufficient to maintain the soil near field capacity until mid or late May. Summer rainfall, however, was deficient, so that severe or moderate droughts occured by early July in all years. Total June rainfall averaged only 1 inch, or 3 inches below normal, for each of these years.

On July 19–22, 1953, stand I received nearly 5 inches of rain, which recharged the soil to a depth of 2 or 3 feet. On July 18–19, 1954, the stand received 2 inches of rain; this amount recharged less than a foot of soil. On July 13–16, 1955, 5 inches recharged about 3 feet of soil in stand I. Finally, on July 8-9, 1956, 3 inches of rain recharged more than a foot of soil in stand II.

Following these July rains, conditions the first 2 years were again dry for the remainder of the growing seasons. In both 1955 and 1956, however, several inches of rain fell in August and again in September.

Results

A hardwood understory strongly increases the rate of soil-moisture depletion (Fig. 2). All depletion curves for water in the surface 4 feet of soil begin together, near field capacity, in May and early June. By mid-July of each year, the treated is well above the control: 3.5 inches, or 85 percent, greater in 1953; 2.4 inches, or 59 percnt, greater in 1954; 1.0 inch, or 14 percent, greater in 1955; and 3.3 inches, or 69 percent greater in 1956. Then, by late September, the quantitative difference between the curves is much less than in midsummer, and the curves tend to come together again.

Water depletion from the burned plots (1956 data) appears to be less than from the controls, but greater than from the plots with the understory completely removed. Transpiration from the hardwood leaf area put out by rootstock sprouts is a possible reason for this intermediate position of moisture depletion. By mid-July soil moisture under the burn was 1.1 inches, or 23 percent, greater than under the control. By the end of September, however, there was no longer any difference between the two.

Statistical tests. Adequate data were obtained in all years except 1955 for statistical

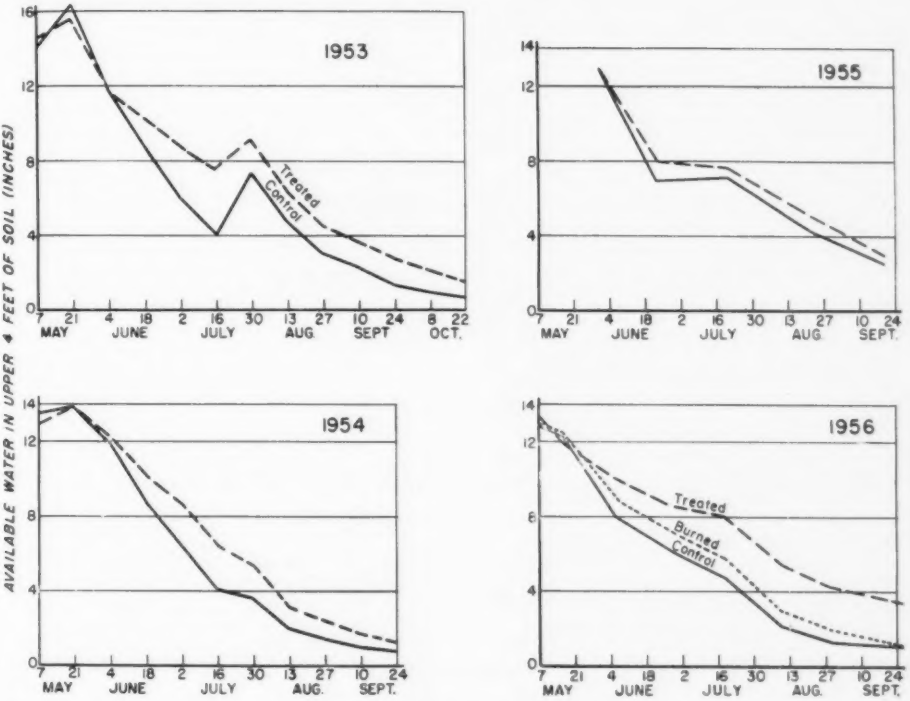

FIGURE 2. *Soil moisture depletion from pine stands with the hardwood understory removed (treated) and left in place (control). The 1956 data include a fire treatment.*

tests of differences in depletion rates. Each year depletion was equal until early June on both treated and control plots, but the two curves began to separate thereafter. A parabolic function was fitted by the method of least squares to each set of data. In 1953 depletion trends were seriously interrupted by the July recharge, which distorted true fits of the data when single curves were calculated for the whole summer. Thus in 1953 the data were tested only through July 16. In 1954 and 1956, curves were fitted through September, regardless of rainfall. Data for the 1956 burn treatment were not analyzed statistically.

A quadratic of the form $Y = b_0 + b_1X + b_2X^2$ was modified to $(y - a) = b_1X + b_2X^2$ with the condition that when $X = 0$, $y = a$, where y = soil moisture, X = 2-week time intervals after beginning of depletion, and a = initial soil moisture content. This function was selected because it simplified comparison of depletion rates, was easy to calculate, and fitted the data closely. Its use does not imply that a simple quadratic function expresses the true relationship between moisture depletion and time.

Treated and control depletion rates within each year were compared statistically by an analysis of the regression coefficients. Tests employing general and common regressions showed that corresponding coefficients were significantly different—at the 1-percent confidence level—for each function (Table 1). The exception is the X^2 coefficients in the 1953 test. However, the slopes of the treated and control curves are significantly different because of the strong

differences between the linear coefficients. Thus from early June to at least mid-July in 1953, and from early June to late September in 1954 and 1956, the rate of soil water depletion of the treated plots was slower than that of the controls.

Discussion. Differences in depletion can best be discussed by referring to various sections of the curves shown in Figure 3. This chart represents generalized trends of the 1954 data, selected for illustration because of least interference from rainfall. The curves from June 4 to September 1 were fitted by the regression equations, while the portions prior to and following this period were drawn by inspection. As long as the soil is near field capacity, sufficient water is transpired by either pine alone (on treated plots) or pine and understory together (on control plots) to meet the requirements of potential evapo-transpiration. This is in agreement with views already expressed by Stone (1952), Thornthwaite and Mather (1955), and Zahner (1955, 1956). The period of equal depletion is represented in Figure 3 by that portion of the curves labeled "a," from May 21 to about June 6.

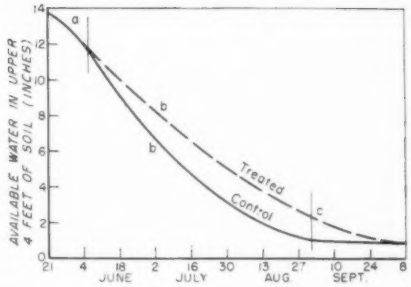

FIGURE 3. *Generalized trends of 1954 depletion.*

TABLE 1. Analysis of variance of difference between corresponding regression coefficients in treated and control equations.

Source	Degrees of freedom	Sum of squares	Mean square
1953 data. Stand I, May 21 to July 16			
X coefficients	1	10.26	10.26**
X^2 coefficients	1	.13	.13
Residuals	4	.87	.218
Total	6	11.26	
1954 data. Stand I, May 21 to Sept. 24			
X coefficients	1	4.42	4.42**
X^2 coefficients	1	4.09	4.09**
Residuals	12	2.04	.170
Total	14	10.55	
1956 data. Stand II, May 17 to Sept. 27			
X coefficients	1	18.47	18.47**
X^2 coefficients	1	4.38	4.38**
Residuals	8	2.67	.334
Total	10	25.52	

**Significant at 1-percent level.

Hardwood and pine roots together probably permeate and occupy the soil to a greater degree than do the pine roots alone. Hardwood and pine crowns together certainly offer greater evaporating surface than do pine crowns alone. The combined effect of overstory and understory is shown in the "b" portion of the curves, where depletion rates indicate that the untreated stand removed soil water 25 percent faster than the treated.

After the water supply becomes very low—portion "c" of the curves—the soil moisture content slowly levels off near wilting point for both treated and control plots. (In 1955 and 1956, September rains kept the treated plots above the wilting point, though the untreated reached wilting point.)

Differences in depletion between treated and control plots were relatively consistent regardless of soil depth (Fig. 4). Although most of the understory roots were concentrated near the soil surface, moisture de-

pletion even at a depth of 4 feet was greatly increased. Water is most easily removed from the zone of least moisture tension (Taylor and Haddock, 1956). Thus, when surface soil moisture is rapidly depleted by pine and hardwood roots together, lower layers also lose water rapidly, even if they are penetrated only by pine roots.

Pine roots alone on the treated plots might eventually permeate and occupy all the soil space formerly shared by pine and hardwood roots. Should this happen, moisture depletion might become more equal on the treated and control plots. The data show a tendency for such to be the case. In stand I, differences in depletion became less each successive year, so that by 1955, five growing seasons after the understory treatment, the treated plots in midsummer contained only 14 percent more moisture than the controls.

Under management, however, a stand will be periodically thinned, thus releasing additional soil space for occupancy by residual vegetation. If understory hardwoods are present, they will respond vigorously, increasing their competitive role. If understory is absent, the freed soil space will be occupied by roots of the overstory pine left after thinning, and the effects of removing the understory may be evident as increased pine growth throughout the life of the stand.

The maximum water-depletion rate from control plots during the hot, dry weather of early June in 1953 and 1954 was about 0.20 inch per day from the surface 4 feet of soil. This is in agreement with measured rates for other forest stands in south Arkansas (Moyle and Zahner, 1954; Zahner, 1955), further supporting the theory that maximum evapo-transpiration from fully stocked forest cover is a constant within a given climatic zone. Data were not sufficient to give an accurate estimate of maximum depletion in 1955, but in 1956 it was again calculated to be about 0.20 inch per day, taking into account both rainfall and soil water storage used in evapotranspiration.

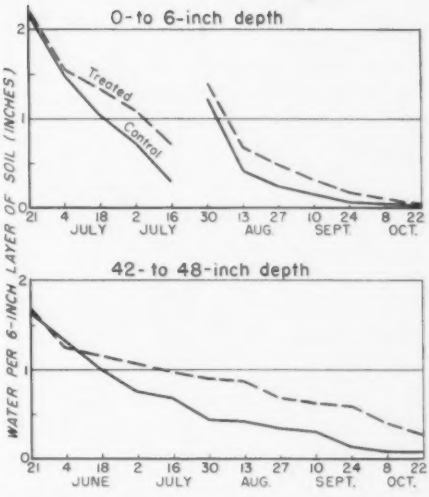

FIGURE 4. *Moisture depletion at two different depths during 1953. These curves are typical of similar depths during other years.*

Summary

Soil water depletion by well-stocked, even-aged pine stands with and without hardwood understories was measured through four summers in southern Arkansas. The hardwood understory was completely eradicated on some plots by chemical means and left undisturbed on others. Another set of plots received two prescribed burns as a hardwood control measure.

Midsummer water loss rates were about 25 percent faster in plots with understory left in place than in those with hardwoods eradicated by chemicals.

While the soil was moist, evapo-transpiration from all treatments was nearly equal. By July, however, as the soil dried, moisture levels in plots with no hardwood understory were more than 50 percent greater than in plots with the understory present. Soil moisture on burned plots was slightly higher than on control plots but

considerably lower than on chemically treated plots.

It is concluded that understory hardwoods compete significantly for soil moisture in upland pine forests of the Midsouth.

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Effects of Photoperiod and Kind of Supplemental Light on Vegetative Growth of Pines

By
R. J. DOWNS
A. A. PIRINGER, JR.

VEGETATIVE GROWTH of many woody plants is known to be controlled by the relative lengths of the daily light and dark periods. In general, long days prolong the growing period and short days inhibit growth and induce dormancy (Downs and Borthwick, 1956; Nitsch, 1957; Vaartaja, 1954 and 1957; Wareing, 1950). The details of the response to photoperiod, however, vary markedly with species (Downs and Borthwick, 1956). In addition, the photoperiodic response of a given species depends upon the geographic origin of the seeds or other propagating material (Pauley and Perry, 1954; Vaartaja, 1954; Wassink and Wiersema, 1955).

A study was made at Beltsville, Maryland, during the period June 1956 to June 1957 to determine the photoperiodic responses of several species of pine, including where possible individuals of the same species produced from seeds from different geographic areas. The stem-elongation effects of far-red-radiant energy on several kinds of herbaceous plants (Downs *et al.*, 1957; Downs *et al.*, 1958) led us also to investigate lamps having different far-red emission characteristics as sources of supplemental light.

Materials and Methods

The species and varieties of pine used in these investigations along with the origin of each seed lot, are listed in Table 1.

Seeds of all species were germinated in Petri dishes on blotters soaked in tap water. After germination they were transplanted to community flats of peat moss and moved to the greenhouse, where they were grown under long-day conditions obtained by interrupting the naturally occurring dark period with a 3-hour period of low-intensity light from incandescent-filament lamps (Downs and Borthwick, 1956; Wareing, 1950; Zahner, 1955). After the cotyledons had expanded each seedling was potted in a 2-inch clay pot of soil. Uniform seedlings selected about 2 weeks after potting were placed on photoperiods of 8, 12, 14 and 16 hours, on natural daylengths plus a 3-hour interruption near the middle of each dark period and on continuous light.

All plants on 8-, 12-, 14- and 16-hour photoperiods were kept on trucks moved from a dark room into the greenhouse at 8 a.m. each day. At 4 p.m., after 8 hours of natural light, the trucks were moved into ventilated chambers, where for various periods the plants received supplemental light from 100-watt incandescent-filament

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TABLE 1. Species, varieties and origin of seed.

Species[1]	Seed Lot No.	Origin
Ponderosa pine (*Pinus ponderosa* Laws.)	29	Kaibab National Forest, north of Grand Canyon, Ariz.
Ponderosa pine	5	Blacks Mountain Experimental Forest, Lassen County, Calif.
Ponderosa pine	31	Baker district, Wallowa-Whitman National Forest, Ore.
Arizona pine (*P. ponderosa* var. *arizonica* (Engelm.) Shaw)	27	Catalina Mountains, 20 miles northeast of Tucson, Ariz.
Loblolly pine (*P. taeda* L.)	40	South Coastal Plain, North Carolina
Loblolly pine	46	Sussex County, Delaware
Virginia pine (*P. virginiana* Mill.)	3	Beltsville Experimental Forest, Prince Georges County, Md.

[1]Binomials are those used by Little (1955).

lamps. An additional 16-hour photoperiod was used in which the supplemental light was obtained from 30-watt standard cool white fluorescent lamps. After receipt of the supplemental light the plants remained in darkness until 8 a.m.

The plants on natural daylengths plus a 3-hour light interruption near the middle of the dark period, or on continuous light were left in the greenhouse continuously. Thus, these plants received more than 8 hours of natural daylight even on the shortest days of winter. Both the dark-period interruption and the supplemental light for the continuous light treatment were obtained from 100-watt incandescent-filament lamps. The supplemental lights, regardless of type, were so arranged as to provide an illumination of about 30 fc.

Data obtained from the plants on interrupted dark periods are plotted in Figure 1 as equivalent to what would have been obtained on a 20-hour photoperiod. Although such equivalence is valid for some woody plants, such as *Weigela florida*, it is not necessarily valid for pines and is used here only as a way of comparing 16-hour photoperiods, interrupted dark periods and continuous light.

Results

General observations

The main axis of pine seedlings from the cotyledonary node to the first terminal bud is juvenile growth, characterized by having acicular leaves rather than the scale-like ones of the adult phase.

In some species of pine acicular leaves and consequently juvenility extend to the first, the second and sometimes the third leaders. In our tests the acicular leaves on the first leader were not as long as those on the portion of the stem between the cotyledons and the position of the first terminal bud (referred to hereafter as the juvenile stem). When acicular leaves appeared on the second leader, they were usually shorter than those on the first leader. The acicular leaves are often referred to as primary needles and the needles themselves as secondary needles, little reference being made to the scale-like ones on the main axis of the adult phase. Since these structures have distinct characteristics, they will be referred to hereafter as acicular leaves, needles and scale leaves, respectively. In the axil of each leaf, whether acicular or scale-like, is a meristem that has the potential of producing a bud, branch or

fascicle (a short branch terminating in one or more needles). In the juvenile phase, the number of the axillary meristems that produce fascicles is generally small as compared with the number produced on the adult portion of the seedling. The number of axillary meristems producing buds or branches seems to be a specific character.

As reported previously for Scotch pine, *Pinus sylvestris* L. (Downs and Borthwick, 1956; Wareing, 1950), daylength was found to govern the ultimate length of the juvenile part of the stem of loblolly, ponderosa and Virginia pine and, to a less extent, the number of fascicles produced on the juvenile growth. This control of juvenile growth is apparently accomplished by controlling the time of formation of the first terminal bud. The increased length of the juvenile stem on certain photoperiods was due to an increase in the number of structures on the stem and to an increase in the distance between the structures, not just to the expansion of a fixed number of structures with photoperiod controlling the distance between them (Figs. 1A and B, 2A and C). For example, loblolly pine seedlings on 8-hour photoperiods averaged 2.5 leaves per millimeter of stem, whereas seedlings on 16-hour photoperiods averaged less than 1 leaf per millimeter of juvenile stem.

Following the formation of the first terminal bud there was a period of apparent dormancy regardless of treatment. On 14-hour or longer photoperiods there was no elongation of the main axis, but the terminal bud continued to enlarge. On photoperiods of 12 hours or less this dormancy seemed real in that no obvious growth or bud enlargement occurred. Finally, after a period of several weeks the terminal buds of plants on photoperiods of 14 hours or longer began to break and a leader elongated. Following leader elongation another terminal bud was formed and the process was repeated. Above 70° F. loblolly plants continued to make flushes of growth for more than 2 years and no cold treatment between flushes was necessary. During the formation of the terminal buds, axillary buds near the base of the terminal ones apparently undergo a change that leads to the production of long branches having the characteristics of the adult portion of the main axis. Measurements of total growth (Figs. 1B and 2B; Tables 2 and 3) included the length of these long branches as well as the total length of the main axis.

The needles develop from a basal meristem and their length is controlled by photoperiod. Thus, on daylengths of 14 hours or more elongation was greater than on daylengths of 12 hours or less (Figs. 1D and 2D). In addition, photoperiod controlled the number of fascicles produced on the juvenile portion of the stem (Figs. 1A and 2A).

Specific responses

The general observations pertained to all species tested, but the details of the response seemed to show definite specific variation.

Pinus taeda. The juvenile growth of loblolly pine followed much the same pattern as reported for Scotch pine (Downs and Borthwick, 1956), more juvenile-stem growth being produced on 14-hour photoperiods than on 16-hour ones (Fig. 1B). The numbers of the structures associated with the juvenile stem, such as the acicular leaves and the fascicles, generally were greatest on photoperiods that produced the greatest juvenile-stem growth (Fig. 1A). However, the relation between juvenile-stem length and number of structures did not hold over a range of photoperiods. For example, juvenile-stem growth was greater on continuous light than on 16-hour photoperiods, but the numbers of acicular leaves and of fascicles produced on the juvenile stem were the same under the two conditions. The length of the needles depended upon photoperiod but in a different way from juvenile-stem growth (Fig. 1D). Photoperiodic control of the length of the acicular leaves was not so clear-cut (Fig.

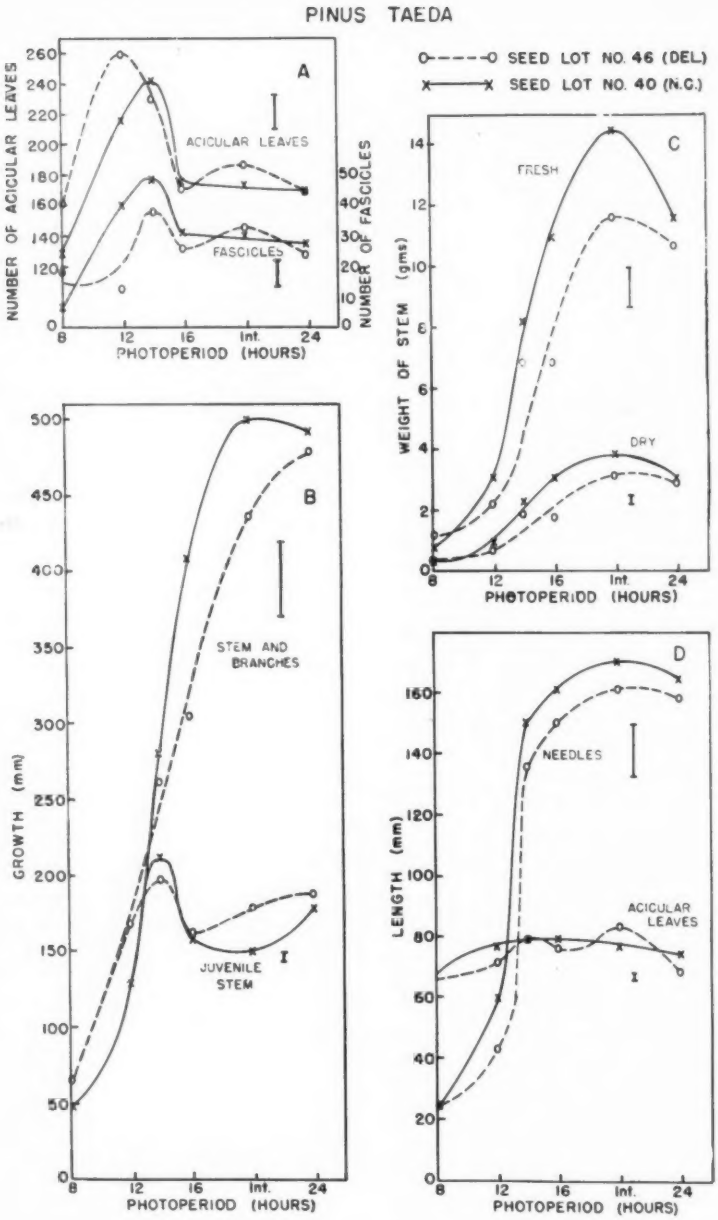

FIGURE 1. *Effect of photoperiod on the vegetative-growth responses of loblolly pine plants from seeds from two geographic areas. The vertical bars (L.S.D. 5%) compare photoperiods and seed lots for the items nearest each.*

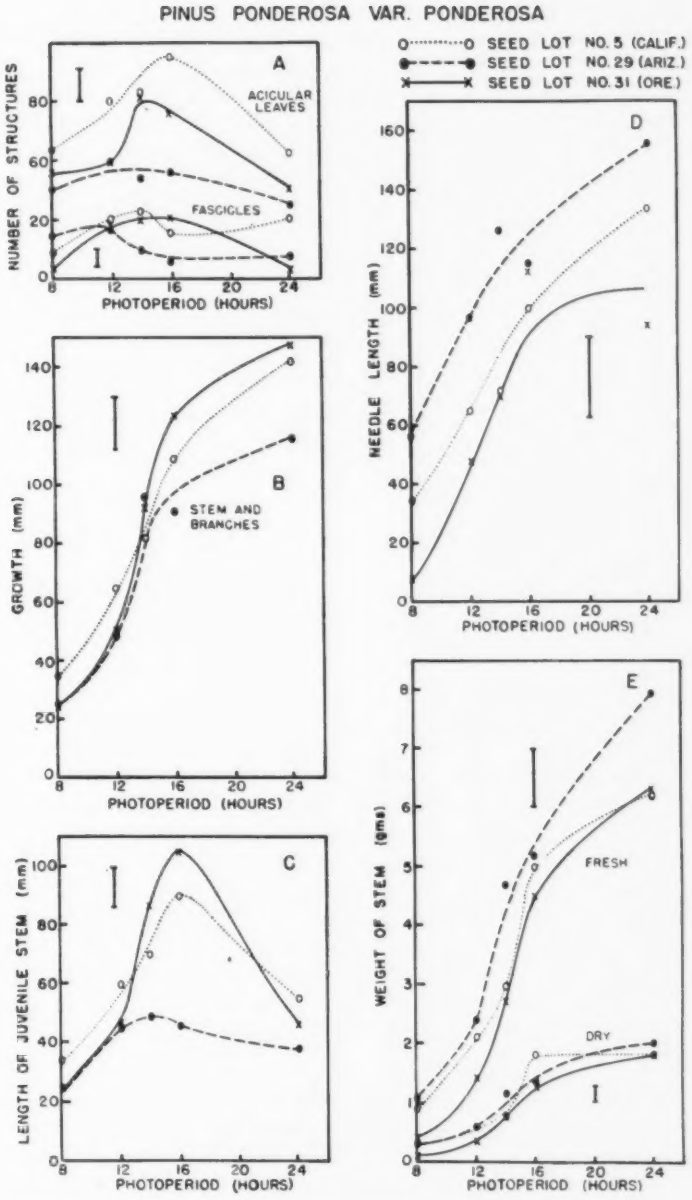

FIGURE 2. *Effect of photoperiod on the vegetative-growth responses of ponderosa pine plants from seeds from three geographic areas. The vertical bars (L.S.D. 5%) compare photoperiods and seed lots for the items nearest each.*

TABLE 2. Effect of photoperiod on the growth of plants of Pinus ponderosa *var.* arizonica.

Photoperiod	Growth[1]		Acicular leaves		Fascicles		Stem		
							Weight		
	Juvenile	Total	Number	Length	Number	Length	Fresh	Dry	Diameter
	mm	*mm*		*mm*		*mm*	*gm*	*gm*	*mm*
8 hours	27	30	66	37	15	88	1.6	0.4	2.1
12 hours	91	94	99	49	12	99	3.1	0.9	2.8
14 hours	77	116	82	43	6	119	3.6	0.9	2.8
16 hours:									
Fluorescent supplemental	41	67	72	45	5	148	4.4	1.2	2.6
Mazda supplemental	53	128	57	39	6	180	5.2	1.5	2.9
Interrupted dark period	48	96	52	44	7	183	5.6	1.8	2.9
Continuous	62	156	62	44	8	198	7.6	2.1	3.0
L. S. D. 5%	20	21	16	10	6	52	1.2	0.4	0.4

[1] Juvenile growth was the length of the main axis from the cotyledons to the position occupied by the first terminal bud, and total growth was the total length of the main axis plus the length of all branches.

1D). The acicular leaf growth on plants from seed lot No. 40 (North Carolina) was equally sensitive to 12, 14 and 16 hours, whereas plants from seed lot No. 46 (Delaware) produced the longest acicular leaves on interrupted dark periods and next longest on 14-hour photoperiods (Fig. 1D).

Additional experiments were made with plants that had been grown 1 year at the Beltsville Experimental Forest. These plants were lifted in the fall and placed in cold storage until February, when they were potted in clay pots of soil and placed in the greenhouse at 70° F. on long photoperiods obtained by a 3-hour interruption of the naturally occurring dark period. When the terminal buds had broken, the plants were divided into equal lots and each lot was placed on a different photoperiod. The growth of these plants on the various photoperiods was similar to the total growth obtained from seedling plants, but the appearance of the plants on 12- and 14-hour photoperiods was somewhat different. On 14-hour photoperiods especially, the branches had a larger diameter than the stem below, looked smooth and had few or no fascicles. The smooth appearance was due to the scale leaves being so tightly adpressed as to appear adnate. The second and third leaders had the same characteristic as the branches but to a lesser degree. After exposure to the various photoperiods the plants were returned to the greenhouse bench, where they were placed on the interrupted dark periods. The plants that had been on 16-hour photoperiods showed no change in growth pattern. Those that had been on 12- and 14-hour photoperiods and consequently had abnormal branches reverted to a more normal appearance. Buds axillary to many of the scale leaves on the abnormal growth produced fascicles so that in a few weeks the plants appeared fairly normal. Terminal buds of these branches and the main axis broke and produced normal fascicle-bearing leaders. The plants that had become dormant on 8-hour photoperiods also began to grow and elongate leaders and branches upon transfer to the long-day conditions.

Pinus ponderosa. Ponderosa pine including the Arizona ponderosa responded to photoperiodic treatment in much the same way as loblolly pine even though the two species

grew at quite different rates. Maximum total growth of loblolly pine, for example, reached 50 cm. whereas total growth of ponderosa pine was less than 15 cm. Needle length maxima were 17 cm. for loblolly pine, 15.5 cm. for ponderosa pine and 20 cm. for Arizona ponderosa pine. Ponderosa pine and loblolly pine reacted to photoperiod differently in that ponderosa produced less juvenile growth but greater fresh weight of stems under continuous light than on a 16-hour photoperiod (Figs. 2C and 2E).

Arizona ponderosa pine differed from ponderosa in several ways. The number of juvenile leaves and the length of the juvenile stem of plants of Arizona ponderosa were greatest on 12-hour photoperiods and reductions on 16-hour ones were severe (Table 2). The number of fascicles on the juvenile steam was greater on 8- and 12-hour photoperiods than on other photoperiods, decreasing markedly on photoperiods of 14 hours or more. Fresh and dry stem weights of plants of Arizona ponderosa showed nearly linear responses to increasing photoperiod (Table 2), which in general agreed with the growth of of plants from ponderosa seed lot No. 29 (Arizona).

Pinus virginiana. Like ponderosa pine, Virginia pine produced the most juvenile-stem growth on 12-hour photoperiods (Table 3). The number of acicular leaves and the number of fascicles on the juvenile portion of the stem followed the response of juvenile growth: the longer the juvenile stem the greater the number of structures. Fresh and dry stem weights and stem diameters followed the pattern of total growth by increasing as photoperiods increased. The smallest increase in stem weight and diameter to an increased photoperiod occurred between 8 and 12 hours (Table 3).

Photoperiodic ecotypes. The photoperiodic ecotypes that have been described for other species (Pauley and Perry, 1954; Vaartaja, 1954; Wassink and Wiersema, 1955) also seem to occur in loblolly and ponderosa pines. Measurements of growth under the various photoperiodic conditions in January showed marked differences ("F" value 30.00) in the response of plants from seeds from different geographic areas. Essentially, these differences were a measure of the differences in amount of juvenile-stem growth; so measurements were repeated in June of the same year to obtain a measure of how the adult phase reacted. Although the differences in the growth of the plants from different seed lots were still highly significant, the "F" value was now only one-third that obtained 6 months earlier.

In general, on photoperiods of 16 hours or more ponderosa pines from the northern seed lot made more stem growth than those from the southern seed lot (Fig. 2). However, the reverse was true with loblolly

TABLE 3. Effect of photoperiod on the growth of plants of Pinus virginiana.

Photoperiod	Growth[1]		Acicular leaves		Fascicles		Stem		
							Weight		Diameter
	Juvenile	Total	Number	Length	Number	Length	Fresh	Dry	
	mm	*mm*		*mm*		*mm*	*gm*	*gm*	*mm*
8 hours	71	71	137	31	21	49	1.2	0.5	1.9
12 hours	116	116	227	49	48	76	3.1	1.1	2.5
14 hours	106	228	162	34	44	93	8.9	2.6	3.6
16 hours	109	494	154	38	40	116	12.9	3.7	4.1
L. S. D. 5%	35	57	48	4	18	12	1.2	0.4	0.3

[1] Juvenile growth was the length of the main axis from the cotyledons to the position occupied by the first terminal bud, and total growth was the total length of the main axis plus the length of all branches.

pine; the plants from the southern seed lot made more growth than those from the northern lot (Fig. 1).

Effect of supplemental light of different qualities

The vegetative growth of herbaceous plants on long photoperiods is known to vary with the type of light used (Downs *et al.*, 1958). Further, the variation is known to be due to the ratio of red and far-red radiant energy emitted by the light source. The fluorescent lamp emits a very low amount of far red compared with red, whereas the incandescent lamp emits a high proportion of far red to red radiant energy (Downs *et al.*, 1958). Since exposure to far red at the beginning of the dark period induces internode elongation in herbaceous plants (Downs *et al.*, 1957), it is not surprising to obtain greater stem length of pines with incandescent supplemental light than with fluorescent even though both sources apparently satisfy the photoperiodic requirement. Every response measured for loblolly pine showed a significant increase due to use of incandescent rather than fluorescent supplemental light (Fig. 3B). The greatest increase (over 100 percent) was in total growth and the smallest increase (about 14 percent) was in needle length. Plants of ponderosa from two seed lots showed similar responses, but the differences were less (Fig. 3A). The greatest increase (about 90 percent) due to incandescent supplemental light occurred in the juvenile-stem growth of plants from seed lot No. 31 (Oregon) and the smallest increases, not significant, occurred in the fresh and dry weights of the stems of the plants from seed lot No. 31 and in needle length of plants from seed lot No. 29 (Arizona).

In neither species did plants from seed of different geographic areas exhibit equal response to light source, but no regular pattern could be recognized. Juvenile-stem growth of loblolly pine was greater in plants from seed lot No. 46 (Delaware), but other measures of the response tended to be smaller (Fig. 3B). Except for needle length, the differences between plants from seed of different geographic origin were significant only under supplemental light from incandescent sources.

Responses of ponderosa pines from the two seed lots tested differed significantly under both incandescent and fluorescent supplemental light sources when juvenile-stem growth or total growth was used as a measure of the response (Fig. 3A). Fresh and dry stem weights and needle length obtained under the two kinds of light sources showed no significant differences due to geographic origin of the seeds.

Conclusions

In gross aspect, pine species seem to respond to photoperiod in the same way. In general, they produced the greatest juvenile-stem growth and largest number of acicular leaves on photoperiods of 14 to 16 hours. They made greater total growth, fresh and dry weights of stem, and greater needle length on continuous light than on 16-hour photoperiods.

Wareing (1950) reported that growth of Scotch pine decreased when the photoperiod exceeded 20 hours. Since he was working with first-year seedlings, his results were presumably obtained from measurements of the juvenile-stem growth. An earlier experiment at Beltsville with Scotch pine (Downs and Borthwick, 1956) and the present results with loblolly and ponderosa pines agree with Wareing's (1950) results in principle, but not in detail since a 20-hour photoperiod was not tested. Juvenile-stem growth of loblolly was greatest on 14-hour photoperiods and that of ponderosa on 16-hour photoperiods.

A more important feature of the present results was that maximum total growth was obtained under continuous light, indicating that a period of darkness is less important to the adult phase of growth than to the juvenile phase.

Differences in the details of the response of different species may, of course, be at-

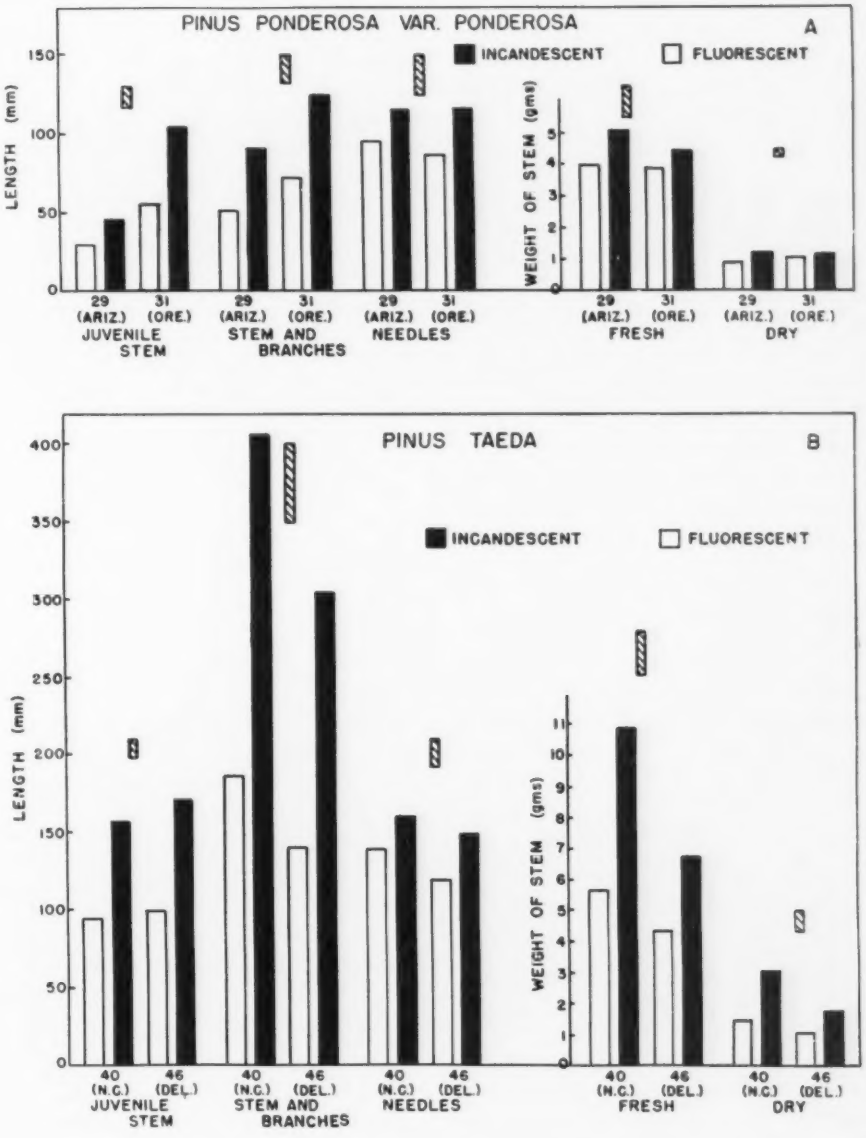

FIGURE 3. *Influence of kind of supplemental light on the vegetative growth of ponderosa pine plants from seeds from two geographic areas (A) and of loblolly pine plants from seeds from two geographic areas (B). All plants received 8 hours of natural light plus 8 hours of supplemental light. The vertical crosshatched bars (L.S.D. 5%) compare light sources and seed lots.*

tributed to the geographic source of the seeds. However, seemingly there is greater variation in response between species than between different seed lots of the same species. This is perhaps best illustrated by the responses of ponderosa pine (seed lot No. 29, Arizona) and Arizona ponderosa pine.

To suggest that the ecotypes of loblolly and ponderosa pines are due to differences in sensitivity to photoperiod necessitates an explanation of the decreasing differences over a period of time of the total growth of plants from different seed lots. The "F" value indicating these differences was essentially a measure of juvenile-growth differences when measurements were made in January, whereas the lower "F" value obtained in June was a measure of total growth differences. Although this decrease in "F" value was due in part to an increased error variance, an examination of the plant material in conjunction with the statistics indicated that it was mainly due to a difference in plant response to treatment. If the ecotype response was due to photoperiod alone, previous reports (Wakely, 1954) would not have predicted such a decreasing difference in response of the plants from seed of different geographic areas. A reasonable explanation is that the plants from seed of different geographic origin are also reacting to temperature in different ways. As the temperatures in the greenhouse increased from the minimum 70° F. to uncontrollable summer maxima often in excess of 90°, the differences between plants from the different seed lots decreased. While not experimental evidence per se, the results nevertheless suggest that photoperiodic ecotypes also react to temperature in different ways and thus lead to the postulation of temperature-photoperiodic or physiological ecotypes.

The response of pine seedlings to supplemental light of different qualities adds further evidence to the existence in pine of the same red-far-red photoreaction that controls many other light-regulated plant responses such as vegetative growth of herbaceous plants (Downs *et al.*, 1957); (Downs *et al.*, 1958), germination of seeds (Toole *et al.*, 1956), coloration of fruits (Piringer and Heinze, 1954), and flowering of both herbaceous (Borthwick *et al.*, 1952) and woody plants (Nitsch, 1957). Perhaps more important at present, these results offer a partial explanation for the different growth rates obtained by different investigators. Certainly future investigators will need to select light sources with some forethought to obtain the type of plant and rate of growth suitable for their particular needs.

Summary

The photoperiodic responses of plants of Virginia, loblolly, ponderosa, and Arizona ponderosa pines were tested. Plants of ponderosa pine came from three seed lots differing in geographic origin: those of loblolly pine from two such seed sources and those of Virginia and Arizona ponderosa pine from one seed source each.

All species were grown on photoperiods of 8, 12, 14 and 16 hours and selected species were also placed on continuous light and on natural days with interrupted dark periods. In addition, loblolly and ponderosa pines from two seed lots each were placed on 16-hour photoperiods obtained by supplementing the basic 8-hour light period with 8 hours of light from a fluorescent source. Incandescent-filament lamps were used as a source of artificial light for all other photoperiods that required supplemental light.

Although the general aspect of the photoperiodic response was the same in the several species tested, the details of the response differed between species and between plants of the same species that originated from seed of different geographic areas. Loblolly and Virginia pines seemed to be more responsive than ponderosa pine to photoperiod differences.

Ponderosa plants from different seed lots tended to respond differently to photoperiod; on long days the northern ones

made the greatest growth. Plants of loblolly pine, however, tended to respond in the reverse manner; on long days the plants from the southern seed source grew most vigorously.

The "F" value indicating differences in response depending upon the geographic origin of the seed decreased when greenhouse temperatures increased. This led to the postulation of temperature-photoperiodic ecotypes.

Differences in growth on 16-hour photoperiods depended on type of supplemental light used. For example, total growth of loblolly pine grown in incandescent supplemental light was as much as 110 percent and ponderosa pine 90 percent greater than the total growth made under the fluorescent supplemental light.

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Tolerance and Photosynthetic Adaptability to Light Intensity in White Pine, Red Pine, Hemlock and Ailanthus Seedlings

BY
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TOLERANCE, in the silvical sense of the term, is merely the ability of a plant to survive and grow under the shade of a forest canopy. Much has been said as to the environmental factors involved in the concept of tolerance and their relative importance. It seems safe to conclude with Shirley (1945) that, at each level of root competition, light limits growth, and, conversely, that at each level of light intensity, removal of root competition stimulates growth. Light may also be operative through its indirect effect on root development. For instance, pine seedlings in the Southeast Piedmont do not survive well in the shade, presumably because reduced photosynthesis prevents adequate root growth; hence the high mortality in summer droughts (Kramer and Decker, 1944). Even within the crown of a tree, death of low, shaded branches may be due not only to inadequate illumination but also to an unfavorable supply of water and mineral nutrients.

Considering primarily the light factor, the basic causes of tolerance, as cited by Baker (1950), are: (1) the ability to maintain a relatively high photosynthetic efficiency in weak light, due to mechanical, morphological, or purely physiological adaptations; (2) a favorable distribution of photosynthate in which most goes to the building of "functional" parts of the plant, such as greater leaf area or greater food reserves; juvenile growth of intolerant species is rapid and food stores are low; (3) an inherent vigor, making life possible at a low metabolic level; in some intolerant species it seems that survival is contingent upon a certain minimum growth rate, i.e., there is a negative correlation between dry weight increment and mortality. In this latter connection, Went (1957) mentioned that typical shade plants usually grow slowly and do not use up much sugar, a fact that he suggested might be more important than the greater photosynthetic efficiency in weak light.

The present study is limited to a consideration of the first one of these possible causes of tolerance, photosynthetic adaptation to low light intensity. The anatomical and physiological differences between sun plants and shade plants have long been recognized and studies on aquatic plants made it possible to separate the light factor from

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the root and competition factors. This discussion, however, will be limited to land plants and more especially to forest trees.

There are a number of reports on the effect of light intensity on the photosynthetic rate of leaves of forest tree species, but the information accumulated is sometimes conflicting. The references quoted here are concerned with the photosynthetic behavior of either sun or shade plants (phylogenetic differences), or of leaves grown in the sun or shade (ontogenetic differences).

Dealing with the first of these two topics, Burns (1923) compared the light compensation points (light intensity at which photosynthesis and respiration balance each other) of tolerant and intolerant species. In general the latter were found to have a lower compensation value, which would indicate a greater photosynthetic efficiency in weak light. For instance, the compensation point in sugar maple (*Acer saccharum* Marsh.) was reached at 2.1 percent of full sunlight (December insolation in Vermont), in eastern hemlock (*Tsuga canadensis* (L.) Carr.) at 4.7 percent, in eastern white pine (*Pinus strobus* L.) at 5.8 percent, and in Scotch pine (*Pinus sylvestris* L.) at 15.9 percent. On the other hand, Stålfelt (1921) found compensation values of 7.5 percent full sunlight for Norway Spruce (*Picea abies* (L.) Karst.) and only 4.0 percent for Scotch pine, although spruce is more tolerant. Grasovsky (1929) found no difference in minimum intensities necessary for survival of hemlock, white pine, or red pine (*Pinus resinosa* Ait.). Bates and Roeser (1928) stated that redwood (*Sequoia sempervirens* (D. Don.) Endl.) theoretically could survive at less than 1 percent of full sunlight whereas white pine, red pine and pinyon pine (*Pinus edulis* Engelm.) would require, respectively, 2.0, 2.6, and 6.3 percent full sunlight.

Curves expressing the photosynthetic rate of shade plants as a function of light intensity generally have a steeper initial slope than those for sun plants. The light intensity at which the curve reaches a maximum value (saturation intensity) as well as the magnitude of this maximum (saturation rate) are also lower. This was found by Stålfelt (1921) in comparing Scotch pine and Norway spruce and, recently, has been established by Böhning and Burnside (1956) for a number of herbaceous species.

Lower maximum rates of photosynthesis may not be as meaningful, in terms of tolerance, as lower saturation intensities. As Decker (1955) pointed out, a given rate of apparent photosynthesis, expressed in absolute units, may have a quite different meaning in terms of survival and growth for different species. Consequently, the safest way to compare plants of different species may be to equate the maximal photosynthetic rates and to express all rates as percentages of the observed maxima. This procedure was used by Kramer and Decker (1944) to show that climax hardwood species of the Piedmont of the Southeast were more efficient at low light intensities than successional loblolly pine (*Pinus taeda* L.), and by Bourdeau (1954) in comparing climax oak species in the same region.

Investigations comparing the photosynthetic behavior of sun-grown and shade-grown leaves have generally revealed differences similar to those found between sun and shade plants.

Boysen Jensen (1929) reported that sun leaves of European beech (*Fagus sylvatica* L.) and European ash (*Fraxinus excelsior* L.) had higher compensation points than shade leaves of the same species, as well as higher saturation intensities and higher saturation rates on a unit-area basis. Tranquillini (1954) found that shade leave of European beech had their compensation point at 50 lux (5 foot candles) as compared to 300 lux (28 foot candles) for sun leaves. Burnside and Böhning (1957) described adaptations to weak light (lower compensation point, lower saturation intensity) in several species of typical sun plants (beans, cotton, and tobacco) when grown in deep shade. Some species, however, reacted in

the opposite direction (tomato had a higher compensation point). Wassink *et al.* (1956) found "typical" adaptation in sycamore maple (*Acer pseudoplatanus* L.): light curves of leaves adapted to low light intensities were of the "Blackman type," i.e., had the same initial slope but different saturation levels, whereas leaves adapted to high light intensities yielded curves of the "Bose type," which had different initial slopes as well as different saturation levels.

Working with a conifer, Iwanoff and Kossowitsch (1929) reported lower maximum rates of photosynthesis, per unit-area, in shade-grown needles of Scotch pine than in sun needles. Stålfelt (1921), however, found lower compensation points in shade needles of Norway spruce and Scotch pine but the maximum rates, per unit of fresh needle weight, were greater in shade needles and both types of needle had the same saturation light intensity. Tranquillini (1955) observed lower compensation points in shade-grown needles of *Pinus cembra* L. Bormann (1956a) presented data for loblolly pine which indicated that, at low light intensities, shade-grown seedlings had greater photosynthetic rates, based on dry weight of leaves, than sun-grown seedlings, but the differences were not significant.

By and large, it seems that tolerant species and shade-grown leaves are more efficient in weak light but less efficient in strong light than intolerant species and sun-grown leaves. There are, however, several exceptions to this general rule. Also, the differences in leaf physiology induced by shading vary from species to species.

Therefore, it was thought desirable to compare the photosynthetic behavior of leaves of certain tolerant and intolerant species grown in full light and under various degrees of shading. Eastern white pine, red pine, and eastern hemlock were selected because of their ecological importance and interest to the Northeast. Here the shade-tolerant hemlock tends to displace white pine. Ailanthus, *Ailanthus altissima* (Mill.) Swingle, was also included as a typical intolerant broad-leaved species.

Materials and Methods

The white and red pine seed used was of Adirondack origin, the hemlock seed came from Connecticut and the ailanthus fruits were collected locally. After stratification for 60 days at 4° C., the pine and hemlock seeds were germinated in flats in a greenhouse. Ailanthus samaras did not require stratification.

Shortly after emergence the seedlings were transferred to individual pots and assigned at random to one of four light-intensity regimes: full light, screened by one, by two or by three layers of shading material, designated hereafter as treatments 0, 1, 2, and 3. At noon, on clear days, the light intensity at plant level was equal, respectively, to 100, 30, 5 and 1.8 percent of full sunlight. The lower the light intensity in the open, the higher was the percentage of full light reaching the screened plants. For example, at a light intensity in the open (treatment 0) reduced to 400 foot candles, the light intensity in treatments 1, 2, and 3 was equal, respectively, to 32, 10 and 4 percent of that in treatment 0. Similar relationships have been shown by Bormann (1956b). To maintain vigorous growth through the winter, natural daylight was supplemented by 500-watt incandescent bulbs giving an illumination of 410 foot candles at plant level (without screen) and a 16-hour photoperiod was maintained. Temperature in the greenhouse was not allowed to fall below 15° C. Maximum temperatures and light intensity were inevitably confounded in the treatments, as they are to a great extent under natural conditions. The plants were well watered throughout the entire experiment. Survival, height growth and leaf development were recorded at weekly intervals.

Determination of rates of respiration and photosynthesis under varying light intensities were made when the seedlings were 4 to 6 months old. The measurements were

made on the entire attached shoots in the pines and hemlock, and on detached leaf parts in ailanthus. Preliminary tests indicated that the rate of CO_2 exchange was not altered during the first hour following severing of the leaf rachis if the cut end was placed in water.

The shoots or leaf parts were enclosed in a cylindrical, Lucite chamber connected by plastic tubing to the sample tube of a Model 15-A Liston-Becker infrared CO_2 gas analyzer.

Air was circulated in this closed system at a constant flow of 3 liters per minute. Rate of decrease or increase in CO_2 concentration of the system in the range 270-330 ppm was taken as a measure of apparent photosynthesis or respiration. The light source was a 700 watt Fluomeric[1] lamp which combines mercury arc and incandescent filaments. Light intensity was varied by altering the distance from the lamp to the chamber and by interposing gauze screens. All determinations were made at a controlled temperature of 25 ± .05° C., cooling being achieved by the circulation of cold water in a jacket enveloping the chamber. Determinations of CO_2 exchange were made in the dark, and at 180, 280, 620, 940, 1400, 1900, 2600 and 3500 foot candles on at least six seedlings of each species for each treatment. Prior to being placed in the chamber the plants were submitted to a 45-minute induction period under a light source similar to that used in the apparatus. The schedule was so arranged that an equal number of individuals from each treatment was measured in the morning and in the afternoon. All measurements were started under the highest light intensity.

After removal from the chamber, fresh weights of needles, shoots, and roots of the pines and hemlock seedlings and fresh weights and areas of the ailanthus leaves were determined. Representative leaf samples were taken for determinations of water content by oven-drying, of chlorophyll a and b, using a modification of MacKinney's method (1941), and of nitrogen content by the micro-Kjeldahl method (A.O.A.C., 1955). Anatomical observations were made on sections of leaf material that had been fixed in F.A.A., embedded in Tissuemat and stained in safranin-fast green.

Results and Discussion

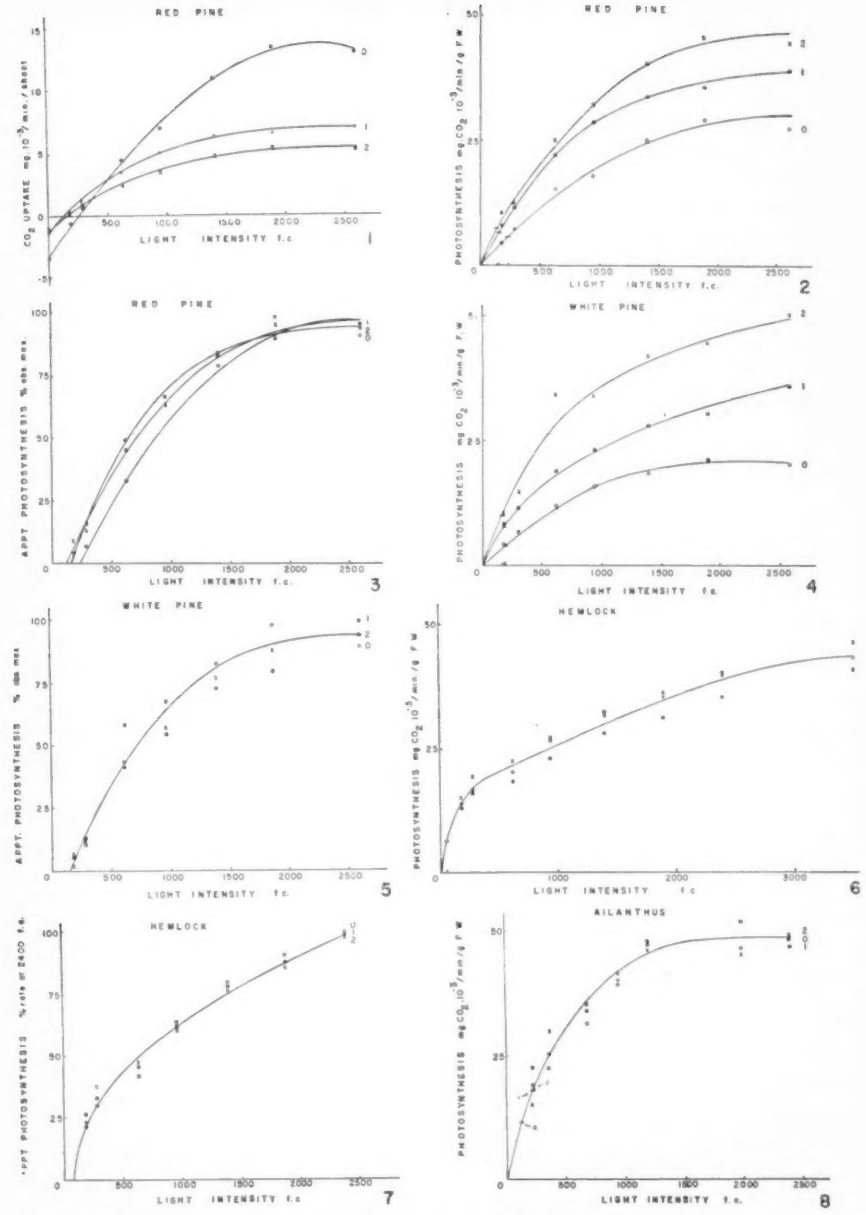
Red Pine. Only two out of 12 seedlings survived in treatment 3 (1.8 percent of full sunlight) and slightly over half survived in treatment 2. Growth was strongly reduced by shading (Table 1). Seedlings in treatment 1 had an average fresh weight equal to 30 percent of that of the seedlings in full light, whereas those in treatment 2 averaged 15 percent. The shoot-root ratio increased with shading from 1.30 in treatment 0, to 4.46 in treatment 1.

Despite the differences in size and weight, average rates of apparent photosynthesis per shoot in weak light (180 and 280 foot candles) were significantly higher in the shade-grown plants. Light intensity had to be raised above 620 foot candles to obtain significantly higher rates in the sun-grown shoots (Fig. 1). The average light compensation point, determined by interpolation, was significantly lower in the shade plants (144 foot candles in treatment 1 vs. 216 in treatment 0).

On the basis of the fresh weight of the needles, average rates of total photosynthesis were greater at all light intensities in the shade plants, the increase being related to the degree of shading (Fig. 2). The superiority of the shade needles was greater in weak light than in strong light as shown by the ratio of CO_2 uptake in shade and sun plants at different light intensities (Table 2).

In view of the higher average water content of shade-grown needles (Table 1) the

[1]Manufactured by Duro-Test Corporation. The emission spectrum has peaks at 4400, 5500, 5800, and 6600 angstroms. One foot candle of this light source as measured with a quartz-window Weston illuminometer is the equivalent of about 25 ergs/cm.^{2}/sec. of visible light.



FIGURES 1 TO 8. *Light curves of photosynthesis in red pine, white pine, hemlock, and ailanthus seedlings grown in full light (0), moderate shade (1), and deep shade (2). Photosynthesis expressed variously as indicated in each figure. Short bars on curves in Figures 2, 4, 6, and 8 indicate CO_2 output in darkness. All curves are drawn freehand.*

differences between shade and sun plants would be accentuated if rates of photosynthesis were expressed on a dry weight basis of the needles.

As mentioned before, there is some advantage in using relative rates, as percentages of observed maxima, in comparing different species. The same reasoning may apply to plants of the same species subjected to different treatments. Thus, photosynthetic performance of the red pine seedlings was compared on the basis of the maximum apparent rate for each seedling. Tests of significance were carried out on the angular transforms of the percentage data (Fisher and Yates, 1949). Figure 3 shows that shade plants were superior to sun plants up to and including 940 foot candles. These differences were statistically significant. It can also be seen that maximal rates were attained at about the same light intensity, 1900 foot candles, in all treatments.

All seedlings bore primary and secondary needles. Shade plants developed more slowly and had, on the average, fewer fascicles of secondary needles than sun-grown seedlings. Primary needles in red pine might be more efficient in weak light than secondary needles, as they are in loblolly pine (Bormann, 1956a), but the shade-grown seedlings used in the present study did not have a significantly higher proportion of primary needles, on a fresh weight basis, when the measurements were made. Needle anatomy was not markedly affected by treatment but, on the average, shade-grown secondary needles were somewhat thinner and longer. As a result the average ratio of surface area to volume was about

TABLE 1. Characteristics of seedlings grown under various degrees of shading.[1]

Species	Treatment	Percent full light	Seedling weight (gms.) (fresh basis)	Shoot-root ratio (fresh basis)	Percent needle water content (dry basis)	Total chlorophyll, mg./g. needle (fresh basis)	Chlorophyll, a/b ratio	Percent nitrogen (dry basis)
Red pine	0	100	1.180 *	1.30 *	104 *	1.086 *	1.21	1.37 *
	1	30	.358 *	2.66 *	155 *	1.488	1.20	1.66
	2	5.5	.179	4.46	277	1.571	1.24	1.72
	3	1.8[2]	.096	3.86	----	----	----	----
White pine	0	100	.939 *	.85 *	123 *	1.158 *	.99	.89 *
	1	30	.435 *	2.11	204 *	1.594 *	.98	1.38 *
	2	5.5	.132	2.20	278	3.373	.87	1.89
	3	1.8[3]	.082	4.78	----	----	----	----
Hemlock	0	100	.396 *	2.20	75	1.481 *	1.07	1.22 *
	1	30	.093 *	1.34	79	2.560 *	1.10	1.51
	2	5.5	.036	1.06 *	68	4.036	.96	1.59
	3	1.8	.027	2.21	94	2.903	1.04	1.88

[1]Significant treatment differences (5% level) indica ed by asterisk between average figures.
[2]Average of two determinations only.
[3]One determination.

TABLE 2. Average ratios of total photosynthetic rates (per gram needle, fresh weight) in red pine grown under various shading treatments.

Light intensity (foot candles)	Rate treatment 1 / Rate treatment 0	Rate treatment 2 / Rate treatment 0
180	1.92	2.44
280	1.67	1.78
620	1.59	1.80
940	1.59	1.79
1400	1.35	1.61
1900	1.22	1.58
2600	1.42	1.63

15 percent larger in shade needles. This could facilitate gaseous exchange between needles and the surrounding atmosphere. However, the differences in average photosynthetic rates remained significant when they were expressed on a unit-area basis.

Nitrogen content was slightly but significantly higher in the shade needles but there were no significant differences between treatments 1 and 2 (Table 1). Part of the increase in nitrogen was probably correlated with the increase in chloroplastic material. Respiration rates per gram dry weight were greater in the shade plants. On a unit nitrogen basis, however, the differences became non-significant.

Chlorophyll contents of the needles are presented in Table 1. The amount of chlorophyll per gram fresh weight of needle tissue was significantly greater in the shade plants (treatments 1 and 2) than in the sun plants, whereas the differences between treatments 1 and 2 were not significant. Treatment had no effect on the ratio of cholorophyll a to chlorophyll b. On the basis of dry weight of needles, the differences in chlorophyll concentration between treatments 1 and 2 were significant.

The shade-grown needles contained more chlorophyll and had higher photosynthetic rates per unit weight. As a result, photosynthetic yields per unit amount of chlorophyll, as expressed in Figure 10, were not significantly different among treatments except at the lowest light intensities where the shade plants still had a slight advantage.

The relative constancy in photosynthetic yields per unit amount of chlorophyll observed here are in agreement with the findings of Willstätter and Stoll (1918). They reported that leaves of widely different chlorophyll content had very similar "assimilation numbers," i.e., grams CO_2 uptake/hour/gram of chlorophyll at 45000 lux (4206 foot candles) and 5 percent CO_2 atmosphere concentration.

On the other hand, Gabrielsen (1948) concluded that chlorophyll content could be a limiting factor in weak light only. In 17 types of leaves, photosynthesis at 130 foot candles was linearly related to chlorophyll content if the latter did not exceed 6 mg./100 cm^2 of leaf area. The amounts of chlorophyll found here cannot be compared with his values which pertained to angiosperms only, and were expressed per unit of leaf area exposed to light.

The light curves of the red pine needles are very similar to those given by Emerson (1929) for normal and chlorotic *Chlorella* cells and by Rabinowitch (1956) for a dense and for a dilute algal suspension. The steeper initial slopes and higher maximum rates of the curves for the chlorophyll-rich material were attributed by Rabinowitch to greater light absorption. He also mentioned the possible role, in limiting the maximum rate, of a hypothetical catalyst that would be present at a concentration proportional to that of chlorophyll, but much smaller (about 1/1000 of it).

It seems as though chlorophyll content, with or without any other closely associated factor, is limiting the rate of phytosynthesis of the sun-grown needles of red pine, at high as well as at low light intensity.

This is in contrast with the reports mentioned earlier in which shade-grown leaves of most plants were found to be more efficient in weak light, but less efficient in strong light. Rabinowitch (1951) ex-

plained this behavior by postulating that shade adaptation in these plants involved not only an increase in chlorophyll content, but also a decrease in one or more rate-limiting catalysts. As a result the light curve levels off at a lower rate than in the sun leaves. Sometimes also, prolonged exposure to strong light actually reduces the rate of photosynthesis in shade-grown leaves, as reported by Böhning (1949).

White Pine. As with red pine only one out of 12 seedlings survived in very weak light (treatment 3) and about 50 percent survived in treatment 2. Table 1 shows the decrease in plant weight and increase in shoot-root ratio caused by shading. Seedlings in treatment 1 had a fresh weight equal to 46 percent of those grown under full light, yet photosynthetic rate per plant was about the same in both groups at all light intensities used. Seedlings in treatment 2 were about 14 percent as heavy as those of treatment 0 and their rates averaged slightly less than 50 percent of those in treatment 0.

Thus, on a unit fresh weight basis, shade-grown seedlings had significantly higher rates of total photosynthesis than sun-grown seedlings at all light intensities, the difference increasing with the degree of shading (Fig. 4). The differences were greater for rates per unit dry weight because shade needles had a higher water content (Table 1). Rates of apparent photosynthesis, as a percentage of observed maxima, however, were not significantly different among treatments at any light intensity, although shade plants had a slight advantage in weak light (Fig. 5). The general average compensation point was about 175 foot candles but there were no significant differences among treatments, contrary to the results obtained with red pine. Saturation intensity was reached at 1900 foot candles in the sun plants, whereas photosynthetic rates in shade plants kept increasing up to and including 2600 foot candles.

From treatment 0 to 2, chlorophyll content increased by a factor of 2.9 on a fresh weight basis and nitrogen content by a factor of 2.1 on a dry weight basis (Table 1). The ratio of chlorophyll a and b was not affected by treatment. Respiration rates

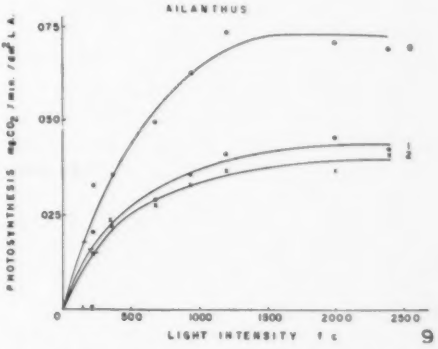


FIGURE 9. *Light curves of total photosynthesis per unit leaf-area in ailanthus seedlings grown in full light (0), moderate shade (1), and deep shade (2). Short bars on freehand-drawn curves indicate CO_2 output in darkness.*

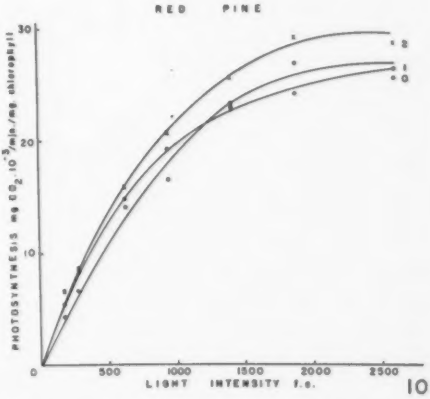


FIGURE 10. *Light curves of photosynthesis yield per unit amount of chlorophyll in red pine seedlings grown in full light (0), moderate shade (1), and deep shade (2). Curves are drawn freehand.*

were larger in the shade plants, even when expressed on a unit nitrogen basis.

As in red pine, the seedlings grown under shade had fewer secondary needles than the sun plants and these were somewhat longer and narrower. Needle anatomy, however, was not seemingly affected by shading.

Although the shade-grown needles were only slightly more efficient in weak light, their absolute rates per unit of weight were greater at all light intensities than those of the sun-grown needles. As in red pine, photosynthetic yields per unit amount of chlorophyll were not significantly different among the various treatments. Thus it seems that, here also, chlorophyll content was the limiting factor in the sun-grown needles.

Hemlock. Survival was high even in deep shade (80 percent in treatment 2 and 55 percent in treatment 3) but growth was reduced considerably by exposure to low light intensity (Table 1). Average shoot-root ratios decreased from treatment 0 to 2 and increased from 2 to 3.

Average photosynthetic rates per plant were higher in those grown in full light at all light intensities but rates per unit fresh weight were not significantly different among treatments (Fig. 6). The same was true of respiratory rates.

Rates of apparent photosynthesis, expressed as a percentage of rate at 2400 foot candles (Fig. 7), were slightly greater in the shade-grown plants up to and including 620 foot candles, but not significantly so. Rates at 180 foot candles were equal to at least 20 percent of the observed maximum in all treatments. The compensation point, estimated by interpolation, was reached at less than 100 foot candles in all treatments. There was a substantial decrease in steepness of the light curve around 180 foot candles and rates kept increasing up to, and including, the highest light intensity (3500 foot candles) at which measurements were made.

Chlorophyll content increased from treatment 0 to 2 but decreased from 2 to 3. The water content of leaves was slightly greater in needles grown in very deep shade (treatment 3). Nitrogen content increased slightly from treatments 0 to 3 (Table 1).

There were no obvious differences in leaf morphology between sun and shade plants.

In contrast with red and white pines, hemlock needles showed very little flexibility in their reaction to shading. The light curves were the same in seedlings from all treatments although chlorophyll content generally increased with shading. Thus photosynthetic yields per unit amount of chlorophyll were lower in shade plants. This suggests that chlorophyll was not limiting. In this connection, it may be of significance that chlorophyll content in sun needles of hemlock was about the same as that of shade needles of red or white pine in treatment 1. The relatively large chlorophyll content in hemlock needles might be responsible for the low compensation point and the steep initial slope of the light curve whereas the decrease in steepness of the curve might be due to a deficiency in some other internal factor. No explanation is offered for the fact that saturation light intensity was not reached before 3000 foot candles.

Ailanthus. Compared with those developed in full light, shade-grown leaves were larger but thinner, as indicated by the average values for leaf weight per unit area (Table 3). In contrast with sun leaves, shade leaves had loosely arranged palisade tissue and considerably more air space in the spongy mesophyll. Light curves of photosynthesis were thus quite different, whether the rates were expressed on a unit weight or on a unit area basis. Average rates of total photosynthesis per gram of fresh weight were not significantly different at any light intensity (Fig. 8), but respiration rates per gram of fresh weight were larger in shade leaves (18.4 and 11.5 micrograms CO_2/minute, in treatments 1 and 0, respectively). Rates of photosyn-

thesis per unit of leaf area were considerably greater at all light intensities in sun leaves (Fig. 9). Average compensation point was also lower in sun leaves (150 foot candles versus 200 foot candles in shade leaves). Saturation intensity was about the same in all treatments.

Apparent rates as percentages of observed maxima were not markedly different although sun leaves had a slight but not significant advantage.

Chlorophyll content increased, on a weight basis, from treatment 0 to 2, then decreased slightly. However, as shade leaves were thinner they had less chlorophyll per unit area than sun leaves (Table 3). Nitrogen content increased with shading, on a weight basis (Table 3), but on a unit leaf-area basis the figures were, respectively, 0.066, 0.061 and 0.038 mg. per cm.^{2} for treatments 0, 1 and 2, indicating that most of the decrease in dry weight and leaf thickness produced by shading affected non-nitrogenous components of the leaf.

Ailanthus leaves exhibited a negative adaptation to shade since shade-grown specimens had higher compensation points, lower rates of photosynthesis per unit area throughout the range of light intensity used, and lower relative rates of apparent photosynthesis in weak light. The differences in rates per unit area were due, seemingly, more to differences in leaf thickness than to differences in chlorophyll content. Light curves of sun and shade leaves of ailanthus differed greatly from those for beech (Boysen Jensen, 1929) and sycamore maple (Wassink *et al.*, 1956) mentioned earlier. In the latter two species, shade leaves were found to be more efficient in weak light but less efficient in strong light and had a lower saturation intensity. Beech and sycamore maple are tolerant species whereas ailanthus is typically intolerant; there may be a causal relationship between photosynthetic reaction to shading and degree of tolerance in these broad-leaved species.

Ecological Implications

From an ecological standpoint the positive adaptation to low light intensity exhibited by red pine may mean that shade-developed seedlings would be fairly efficient in weak light; yet, if suddenly exposed to strong light, they would be able to carry on photosynthesis at higher rates than sun-grown plants, provided their chlorophyll content remained constant. Similarly, needles developing in shaded parts of the crown might make significant contributions to the growth of the tree.

TABLE 3. Characteristics of Ailanthus leaves grown under various degrees of shading.[1]

Treatment	Percent full light	Leaf weight, mg./cm.^{2} (fresh basis)	Leaf weight, mg./cm.^{2} (dry basis)	Total chlorophyll, mg./g. (fresh basis)	Total Chlorophyll, mg./cm.^{2} leaf area	Percent nitrogen (dry basis)
0	100	15.7 *	4.1 *	1.422	.0223	1.61 *
1	30	8.4	2.0 *	1.582 *	.0133	3.03
2	5.5	8.0	1.3 *	2.588	.0207	2.96
3[2]	1.8	6.0	.7	1.924	.0115	.....

[1]Significant treatment differences (5% level) indicated by asterisk between average figures.
[2]Average of 2 determinations only.

White pine did not appear to be as capable of using weak light as red pine but rates of photosynthesis, on a leaf-weight basis, were greater in shade-grown plants.

In hemlock, on the other hand, shading did not affect photosynthetic behavior but seedlings from all treatments were much more efficient in weak light than either sun- or shade-grown white and red pines. The compensation point in hemlock was well below 100 foot candles and apparent photosynthesis at 180 foot candles exceeded 20 percent of the observed maximum. Survival of hemlock seedlings in very deep shade was also much higher than in the pines.

These observations are in agreement with the successional trends in southern New England where the tolerant hemlock is now expanding at the expense of white pine. Hemlock seedlings may also be found developing beneath canopies of plantation stands of red pine. Ailanthus seldom, if ever, enters fully-stocked stands, regardless of the species, Thus, as far as these four species are concerned, photosynthetic efficiency in weak light and degree of tolerance are well correlated.

Summary

The objective of the study was to explore the relationship between degree of tolerance and photosynthetic adaptability to light intensity in eastern white pine, red pine, eastern hemlock and ailanthus. Light curves of photosynthesis were determined for leaves of seedlings grown under various degrees of shading.

In both red and white pines, shade needles had higher photosynthetic rates than sun needles on a unit needle-weight basis. Shade-grown red pine needles had a lower compensation point and were relatively more efficient in weak light. No differences in compensation point appeared in white pine.

Light curves of hemlock needles were similar in all treatments. Hemlock was more efficient in weak light than either red or white pine.

Chlorophyll and nitrogen content of the leaves generally increased with shading. Photosynthetic yields per unit amount of chlorophyll were not significantly affected by the shading treatments in the pines. In hemlock they were lower in shade-grown needles. It is suggested that chlorophyll might be limiting in the pines but not in hemlock.

Ailanthus leaves showed a negative adaptation to light intensity. Shade leaves were less efficient than sun leaves, a fact which might be related to the intolerance of the species.

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A Photoreaction in Paper Birch Seedlings

BY
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G. K. VOIGT

DURING THE COURSE of an investigation concerned with competition in seed beds, a marked growth response was observed in paper birch (*Betula papyrifera* Marsh.) seedlings growing in greenhouse flats. The wood flats (16 x 11 x 5 inches) were of three types: (a) no partition; (b) one partition, dividing the box into equal 8 x 11 inch sections; (c) two partitions, dividing the box into four equal 8 x 5½ inch sections.

The flats were filled to within one inch of the top with washed sand and in November, 1956, 80 milligrams of paper birch seed were sown in each. Thirteen days later the cotyledons of the germinating seeds appeared uniformly in all flats and germination was completed in one month. The temperature in the greenhouse fluctuated from night to day between 65-75° F. The seedlings were watered regularly. About one month after germination pronounced differences in seedling growth were noted in parts of some of the flats. Within a given flat some of the seedlings developed secondary leaves and others showed no development beyond the primary leaf stage. The division between the two stages of development was very clear-cut (Fig. 1.). It was then noted that the areas in which the seedlings had developed secondary leaves were lighted by an incandescent street light located about 100 feet from the greenhouse. The sharp division between the sections containing only seedlings with primary leaves and the sections containing seedlings with secondary leaves coincided exactly with the edge of the shadow cast by the side of the flat. The amount of light was measured with a photo-tube recorder (Galston and Baker, 1953) and was determined to be 2 ergs/cm.^{2}/sec. in absolute energy units.

In April, 1957, leaf counts were recorded and the oven-dry weights of 50 seedlings from the lighted and shaded areas were determined (Table 1). Figure 2 shows the response in root and shoot growth in seedlings taken from the lighted and shaded areas. Considerable variation in the leaf development of individual seedlings occurred within the lighted areas where 26 percent of the seedlings remained in the primary leaf stage. Undoubtedly much of this variation can be attributed to genetic differences between seedlings. Fifteen percent of the seedlings in the shaded areas developed secondary leaves but in all cases these were less well developed than corresponding seedlings from the lighted areas. No shaded seedlings were found with more than three secondary leaves.

The literature revealed a number of records of plant responses to light of low intensity (Table 2). Here it may be noted

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The authors are associated with the Department of Northern Affairs and National Resources, Chalk River, Ontario, Canada, and School of Forestry, Yale University, New Haven, Conn., respectively. They wish to express their appreciation to Dr. A. W. Galston, Plant Science Department, Yale University, for use of his photo-cell.

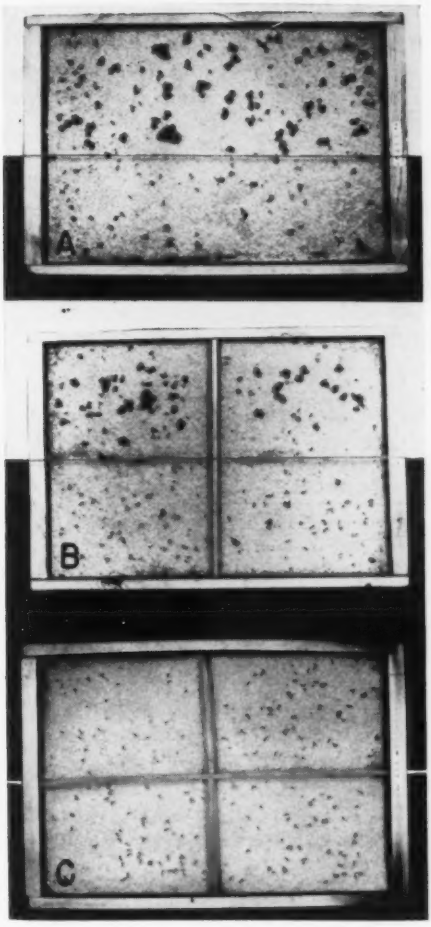

FIGURE 1. *Photoresponse of paper birch seedlings: A, flat with no partitions. String marks boundary of the shadow cast by lower edge of flat. B, flat with partition parallel to path of light. Again string marks the boundary of shadow cast by lower edge of the flat. C, flat with partitions parallel and perpendicular to path of light. Here the lower edge of flat casts a shadow to middle partition, which in turn casts a shadow to the upper edge of flat. Photographs made with camera directly above flat. In all cases the lower edge of the flat in the photograph is nearest the light source.*

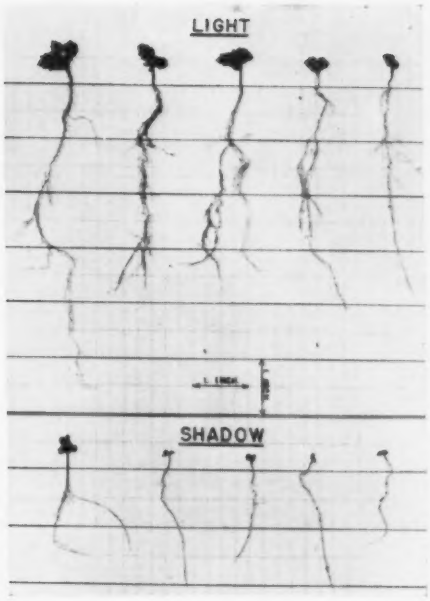

FIGURE 2. *Morphology of paper birch seedlings taken from lighted and shaded portions of greenhouse flats. Note differences in root development.*

that many past measurements of illumination have been recorded as foot candles which express luminous flux or luminous intensity, which, in turn, is related to the light perception of the human eye. Most photo-electric cells in common use are calibrated in foot candles and are, therefore, selective. Because of this, they are subject to the limitations of the visible spectrum, and are not directly related to absolute units of radiant energy. A value for light illumination in foot candles may be converted to units of energy only if the required variables concerning the spectrum of the light source, intermediate factors of light absorption and dispersion, and the range of sensitivity of the recording instrument are known. For comparative purposes, a conversion factor of one foot candle

TABLE 1. Average air-dry weight and leaf development of seedlings growing in lighted and shaded areas of greenhouse flats.

Air-dry weight of 50 seedlings	Percentage of seedlings with primary leaves only	Percentage of seedlings with specified number of secondary leaves				
		1	2	3	4	5
mgm.						
LIGHTED AREAS						
54	26	15	21	22	12	4
SHADED AREAS						
16	84	11	4	1	—	—

TABLE 2. Critical illumination values and calculated energy levels associated with photoreactions in different species of plants.

Author	Species	Illumination	Calculated energy
		Foot candles	*Ergs/cm.²/sec.*
Austin, 1936	*Rudbeckia bicolor superba* (long-day plant) *Cosmos sulphurus* (short-day plant)	Critical values 0.4-1.8 foot candles	10-45
Borthwick and Parker, 1938	Biloxi soybeans	Critical 0.5-1.0 foot candles	12-25
Kramer, 1937	*Abelia grandiflora*	Less than one foot candle 24-hour period	<25
Pauley and Perry, 1954	*Populus* spp.	Minimum employed 1.5 foot candle	37
Wareing, 1950	*Pinus sylvestris*	Maximum number of leaves 20-hour photoperiod at 20 foot candles	500
Withrow and Benedict, 1936	Chinese aster	Critical 0.1 foot candle at 20-hour period	2

equals 25 ergs/cm.²/sec. is used in this report. This value has been calculated from values for full noon sunlight at sea level using 10,000 foot candles and an energy value of 1.5 gm.cal/cm.²/min. (Shirley, 1935). The result of approximately 100 ergs/cm.²/sec. for one foot candle has been arbitrarily reduced to 25 ergs/cm.²/sec. to compensate for changes in light quality and other factors inherent in the foot-candle unit of expression. It is emphasized that this can be only a rough approximation and will provide comparisons of magnitude only.

Assuming an average figure of 13 hours as the length of the natural dark period, the birch seedlings described in this paper were subject to about 13 hours of 2 ergs/cm.²/sec. light radiation in 24 hours, or a total of 9.36×10^4 ergs/cm.² during the period of darkness. A minimum light intensity of 1 percent of full sunlight is re-

quired for effective photosynthesis (Shirley, 1945). Thus the effect observed here is interpreted as a photoreaction resulting from a mechanism other than increased photosynthesis.

It is concluded that the paper birch seedlings showed a significant photoreaction to light of very low intensity which caused a three-fold increase in dry-matter production. The intensity of the light radiation received by the seedlings throughout the night, additional to a normally short day, was somewhat lower than the threshold values previously reported for photoperiodic responses in woody plants.

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Some Anatomical and Physiological Changes In Quaking Aspen Induced by Bark Removal with 2, 4, 5-T

BY
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L. W. REES
R. M. BROWN

PROMISING RESULTS in chemical bark removal of quaking aspen (*Populus tremuloides* Michx.) with the butoxy ethyl ester of 2,4,5-trichlorophenoxyacetic acid have been obtained from two-year field tests at the Cloquet Experimental Forest, University of Minnesota. Application of this chemical to aspen trees outside the bark at breast height during the period of rapid growth resulted in both consistent killing and easy peeling even though the trees were cut in the dormant season. In order to determine why treatment with this chemical caused aspen bark to peel easier, the anatomical and some physiological changes induced by the chemical were studied in comparison with conditions of natural sap peeling.

Wilcox *et al.* (1956) reported the normal changes of peeling resistance of bigtooth aspen (*Populus grandidentata* Michx.) and other pulpwood species during the growing season in New York State. With photographs he showed the development of the cambium in yellow birch and red spruce during various stages of cambial activity. He concluded that the newly formed xylem ruptured easily due to extreme thinness of the cell walls; and, as a result, the bark readily peeled during the period of rapid growth. Raphael (1954) studied the effect of propylene glycol butyl ester of 2,4,5-T on aspen bark and found an advanced disintegration of cambium and a thickening of the cell walls of the phloem parenchyma. Raphael *et al.* (1954) obtained unsatisfactory results with this chemical and concluded that it was ineffective as a bark removal agent.

However, information concerning the anatomical and physiological changes in aspen which influence the ease of peeling under normal development or induced by the butoxy ethyl ester of 2,4,5-T has not been reported. Therefore the objectives of this study were to determine: (a) the natural variation of peeling resistance and moisture content of untreated aspen throughout the growing season, (b) the anatomical changes in the cambium of untreated aspen during various stages of the growing season, and (c) the anatomical and some physiological changes of aspen induced by 2,4,5-T and their effect on peeling resistance.

The authors are Assistant Professor and Professors, respectively, in the School of Forestry, University of Minnesota. Special thanks are due to Dr. F. H. Kaufert and Dr. R. L. Hossfeld for suggestions and comments. This paper is published as Scientific Journal Series No. 3810 of the Minnesota Agricultural Experiment Station, Institute of Agriculture, St. Paul, Minnesota.

Materials and Methods

To follow the changes in untreated aspen throughout the growing season, a sample of five trees was cut each month from April through October in 1955 and the necessary measurements made. To obtain this sample one tree was randomly picked from each of five groups of seven trees selected so the site and stand conditions of each group were as homogeneous as possible. These groups were located in a pure, even-aged merchantable aspen stand approximately 40 years old with diameters from 6 to 10 inches. Treated trees were sprayed at breast height with a diesel oil solution of butoxy ethyl ester of 2,4,5-T in various stages of the growing season. The concentration used was 21 pounds acid equivalent to 100 gallons of diesel oil. Samples of not less than 15 treated trees were cut each month from August to October to determine the changes induced by the chemical. From October to March, when the trees were frozen, no differences could be detected; for this reason only a few test trees were cut during this period.

The following measurements and samples were obtained for each tree. For determining resistance to bark peeling of untreated and treated trees, one measurement was made at the middle of each 100-inch bolt with the Wilcox tool for measuring resistance to bark peeling. These measurements were averaged for each tree and each sample of five trees. To study the anatomical and moisture changes, disks one-inch thick were cut from the base of each 100-inch bolt of each tree. Moisture content based on oven-dry weight for each disk was determined from a composite sample of two sector-shaped sections with the point at the pith and a one-inch arc on the circumference. The anatomical studies were made from slides prepared from samples cut from the disks, killed and fixed with Zirkle's reduced chrome fluid (Johansen, 1940), and embedded in paraffin or celloidin. These sections were stained with haematoxylin and safranin or fast green. Zirkle's fixative and paraffin method of embedding (Lang, 1935) were used to minimize the incidence of artifacts and to preserve the tissue as nearly as possible in its original condition.

To study the change of osmotic pressure induced by the 2,4,5-T, four sapling-size aspen suckers with immature leaves at the top of the branches were selected and two of them given a basal treatment with 2,4,5-T. The other pair was left untreated as a check. After treatment and up to the time the treated suckers died, freehand sections about 50 microns thick were cut at two-day intervals from the growing tip of the branch of each sucker. These sections were placed in a series of sucrose solutions with concentrations varying from 0.300 to 0.500 Molar at 0.025 Molar intervals. The Molar concentration at which plasmolysis begins gives the osmotic pressure of the plant tissue (Bonner, 1952).

The effect of drying on the peeling resistance of chemically-treated aspen trees was also studied. Five trees treated with 2,4,5-T in June, 1956, were cut the following October. From each tree, five bolts one-foot in length were taken at three-foot intervals. The peeling resistance and moisture content of both the wood and bark were measured weekly for four weeks. In order to compare the change in peeling resistance with progressive drying after logging, a 5 x 5 Latin square experimental design was used to eliminate the variation introduced by trees and heights at which the bolts were taken. The bolts were randomly assigned to different dates for peeling resistance and moisture content measurements by using the foregoing design based on five treatments for five trees and five sections.

Results

Changes in peeling resistance and moisture content of untreated aspen during the growing season. The bark peeling resistance and moisture content of untreated aspen vary during the growing season as shown in Figure 1. The significance of the trend was found to be at the 5% level by the F- test. The peeling resistance before growth

started in April was five pounds per square inch and decreased to about one pound per square inch in June. From this minimum it increased to over nine pounds per square inch in October. The lowest portion of the trend line is between May and July which is called the natural sap peeling season because the bark can be easily separated from the wood during this period. The moisture content of the wood was about 100 percent at the beginning of the growing season, but decreased consistently reaching a minimum level in August. It then increased to a higher moisture content rather rapidly at the end of the growing season. Generally a high wood moisture content is associated with high peeling resistance in untreated aspen (Fig. 1). The moisture content of the bark of untreated aspen cut in different months does not differ significantly. It fluctuates from 75 to 90 percent mainly due to the variation in roughness of the bark sampled.

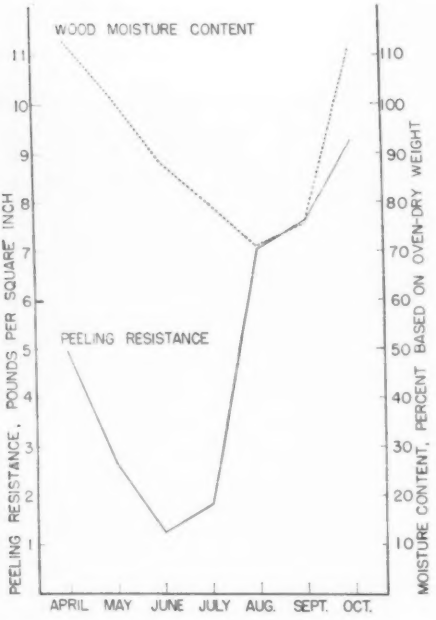

Figure 1. *The peeling resistance and wood-moisture content of untreated aspen for different months during the growing season.*

Anatomical changes during the growing season in the cambial region of untreated aspen. The anatomy of the cambium of untreated aspen trees is quite different in the growing and dormant seasons. Based on this difference three stages of cambial activity may be recognized as follows:

1. The dormant state, from October to April: During this period the cambial cells are distinctly different from the adjacent phloem and xylem elements (Fig. 2 #I). The cambial cells, rectangular in shape, have a smaller vacuole and are compactly arranged in four or five rows. The xylem elements, both fibers and vessels, are heavily lignified with relatively thick cell walls which stain red with safranin.

2. The stage of rapid growth, from May to July: During this stage the cambial cells continue to produce daughter cells that develop into wood and bark elements. Both the cambial initials and the daughter cells have large vacuoles. The daughter cells from the fusiform cambial initials differentiate into vessels and fibers next to the wood; and into sieve tubes, companion cells, phloem parenchyma and fibers next to the bark. The ray initials of the cambium produce isodiametric daughter cells which develop into ray cells in both wood and bark. The cell walls of the newly- formed xylem elements do not stain red with safranin, but stain readily with fast green, indicating that lignin is not present at this time. The walls of these cells are comparatively weak and therefore disrupt very easily. A process of progressive lignification of the cell walls in the older xylem elements is also apparent. This can be recognized by the change in color of the cell walls from green to red across the newly formed xylem when the section is stained with safranin and fast green. Throughout this stage a layer of thin-walled cells is present thus permitting clean separation of the bark from the wood. The structure of the cambial

region is shown in Fig. 2 #II. No distinct difference is apparent between the newly formed daughter cells and the cambial initials. The newly differentiated wood elements, such as vessels and fibers, are still thin walled.

3. The latter stage of cambial activity, from August to the end of the growing season: During this stage the cambial cells stop producing daughter cells. However the lignification of the cell walls of the xylem elements continues. The weak layer of new wood becomes thinner and thinner until finally the secondary thickening and lignification of the cell wall of all wood elements are completed. Under this condition the bark again becomes very difficult to remove.

Anatomical changes of aspen induced by 2, 4,5-T. Aspen trees treated with 2,4,5,-T showed distinct anatomical differences when compared with untreated trees. The treatment prevented the natural sequence of changes within the tree, resulting in the following modifications in structure:

1. Changes in bark structure: Normal mature bark of aspen consists of three major zones: the periderm, cortex and secondary phloem (Chang, 1954). Fig. 3 #I shows a cross section of secondary phloem, cambium and part of sapwood of an untreated aspen. The sieve tubes, irregular in shape, together with the companion cells and the phloem parenchyma are distributed in the spaces bounded by the phloem rays and the tangential bands of phloem fibers. The mature bark elements, except the phloem parenchyma, show no significant response to the chemical when applied in the season of rapid growth. In trees killed by 2, 4, 5-T, the phloem parenchyma adjacent to the cambium multiplies rapidly causing the adjacent sieve tubes to collapse. The non-differentiated meristematic phloem parenchyma develops into an abnormal layer of parenchyma as shown in Figure 3 #II. However, the phloem fibers and rays appear

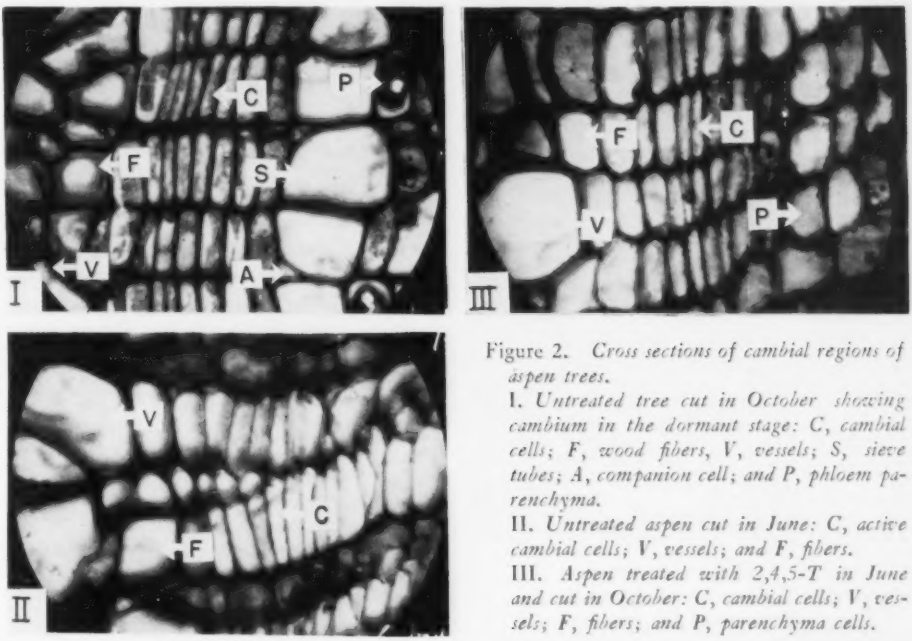

Figure 2. *Cross sections of cambial regions of aspen trees.*
I. *Untreated tree cut in October showing cambium in the dormant stage: C, cambial cells; F, wood fibers, V, vessels; S, sieve tubes; A, companion cell; and P, phloem parenchyma.*
II. *Untreated aspen cut in June: C, active cambial cells; V, vessels; and F, fibers.*
III. *Aspen treated with 2,4,5-T in June and cut in October: C, cambial cells; V, vessels; F, fibers; and P, parenchyma cells.*

unaltered. When aspen is treated in April, the chemical enters the bark in such small amounts that the tree is not killed, but the cambial cells are stimulated by the chemical and grow abnormally. A very thick layer of proliferated parenchyma develops in the bark and even the new-wood elements are distorted (Fig. 3 #III). Since rupturing of the mature bark rarely develops in this proliferated region, the change in the bark structure may not directly account for the ease of peeling induced by the chemical.

2. Changes in wood structure: The new elements, such as vessels and fibers, adjacent to the cambium remain unlignified and thin walled even in the fall. Figure 2 #III shows the cross section of the cambial region of aspen treated with 2,4,5-T in June and cut in October. No distinct difference occurs between the cambial initials and daughter cells. The chemical prevents the development of the secondary wall in the new-wood elements. For the untreated trees this condition is usually found only when growth is rapid. Therefore the prevention of secondary thickening and lignification of the cell wall of the immature-wood elements in treated trees is the main reason why chemically treated trees peel easier. The mature-wood elements produced during the previous season are not changed. However, tyloses are produced abundantly in the vessels by adjoining wood-ray cells as shown in Figure 4.

Change of osmotic pressure in phloem parenchyma cells induced by 2, 4, 5-T. A sample of four aspen saplings was divided into two pairs, and the individuals of each

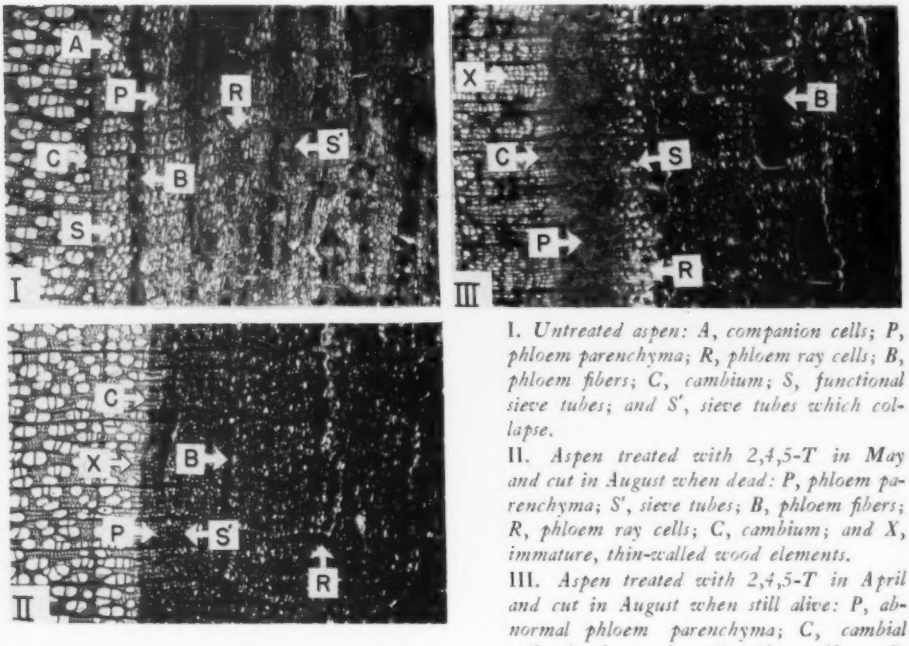

Figure 3. *Cross sections showing anatomy of untreated and treated aspen trees.*

I. *Untreated aspen: A, companion cells; P, phloem parenchyma; R, phloem ray cells; B, phloem fibers; C, cambium; S, functional sieve tubes; and S', sieve tubes which collapse.*

II. *Aspen treated with 2,4,5-T in May and cut in August when dead: P, phloem parenchyma; S', sieve tubes; B, phloem fibers; R, phloem ray cells; C, cambium; and X, immature, thin-walled wood elements.*

III. *Aspen treated with 2,4,5-T in April and cut in August when still alive: P, abnormal phloem parenchyma; C, cambial cells; S, sieve tubes; B, phloem fibers; R, ray cells; and X, distorted new-wood elements.*

pair selected with similar osmotic pressures. One sapling of each pair was treated with 2, 4, 5-T and the other left untreated as a check. The difference in osmotic pressures between the check and treated aspen saplings in each pair was determined at two-day intervals for a period of 20 days. Statistical analyses indicated that this difference changes with time and the trend of this change may be represented by a cubic regression curve (Fig. 5). The difference at the beginning was zero. Two days after treatment the osmotic pressure of the treated aspen started to increase. Six days after treatment the difference in osmotic pressure between the untreated and treated aspen reached a maximum, and thereafter remained almost constant until the treated aspen died. The moisture content of both the wood and bark was higher in trees treated with 2, 4, 5-T than in untreated trees. This increase in moisture may possibly be the result of greater water intake resulting from the increase in osmotic pressure in the cells and the lower water loss because the leaves were killed by the chemical.

Effect of the high moisture content on the peeling resistance of chemically treated aspen. Treatment with 2, 4, 5-T resulted in a lower peeling resistance and a higher moisture content of both the wood and bark. In order to show that the high moisture content is not the cause of the low-peeling resistance, the treated trees were cut and air seasoned for different periods, and the changes in moisture content and peeling resistance determined. The moisture content of both the wood and bark of treated aspen decreased significantly with an increase in length of the seasoning period. The bark with an initial moisture content close to 100 percent based on oven-dry weight when the trees were cut, lost about 30, 50, 60, and 70 percent of the water respectively, after one, two, three and four weeks of drying. The wood lost moisture more slowly than the bark. The bark and wood moisture losses at the end of each drying period are shown in Figure 6. The peeling resistance of treated aspen air seasoned for different drying periods did not differ significantly. However, the apparent trend of peeling resistance is downward

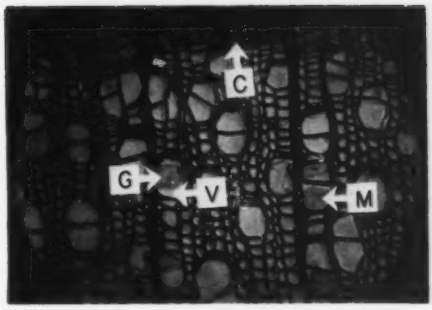

Figure 4. *Cross section of sapwood of aspen treated with 2,4,5-T showing the development of tyloses: G, growing tylosis; M, mature tylosis; V, vessels; and C, cambium.*

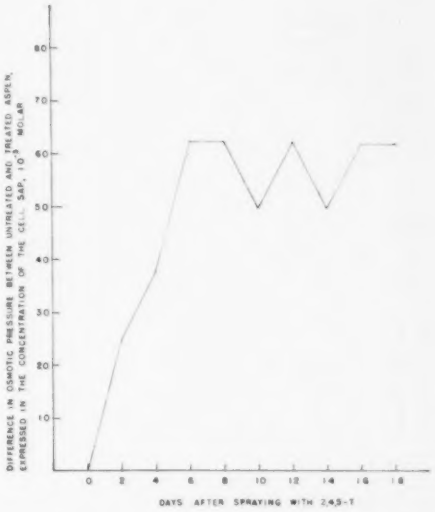

Figure 5. *The difference in osmotic pressure of parenchyma cells between the untreated and treated aspen.*

(Fig. 6). Since the reduction of bark and wood moisture content by air seasoning does not result in a significant change of peeling resistance, the increase in bark and wood-moisture content does not appear to account for the ease with which chemically treated aspen peels. This increase in the moisture content of treated aspen may be considered merely the result of chemical killing.

Conclusions

Both the peeling resistance and moisture content of untreated aspen change with the advance of the growing season. Minimum peeling resistance occurs in the period of most rapid growth because an easily ruptured layer of immature thin-walled wood elements exists next to the cambium. Since untreated aspen shows a higher moisture content of wood in the dormant season, the low peeling resistance is not related to the high moisture content of the wood.

Aspen sprayed with 2, 4, 5-T at breast height during the period of rapid growth peels readily even when the trees are cut in the dormant season. The ease of peeling caused by the chemical is due to the preservation of a layer of immature unlignified and thin-walled wood elements. Treatment with 2, 4, 5-T induced many changes in aspen: an increase in osmotic pressure of parenchyma cells; an increase of the wood and bark moisture content; formation of abnormal phloem parenchyma; prevention of secondary thickening and lignification of the cell walls of the immature wood elements; and development of tyloses in the sapwood.

Loss of water of treated aspen by air seasoning does not significantly change the ease of peeling induced by treatment with 2, 4, 5-T. This further shows that the high moisture content of treated aspen is not the cause of the low peeling resistance.

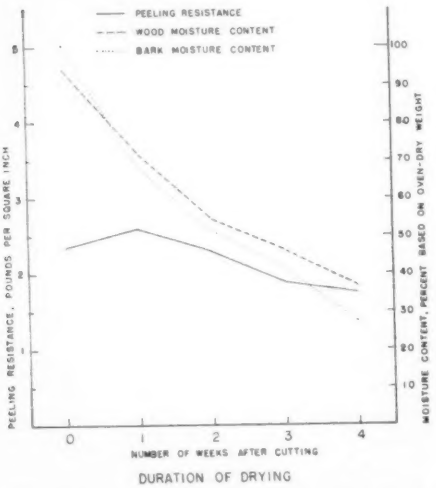
PEELING RESISTANCE
WOOD MOISTURE CONTENT
BARK MOISTURE CONTENT
PEELING RESISTANCE, POUNDS PER SQUARE INCH
MOISTURE CONTENT, PERCENT BASED ON OVEN-DRY WEIGHT
NUMBER OF WEEKS AFTER CUTTING
DURATION OF DRYING

Figure 6. *Variations of the moisture content of wood and bark and peeling resistance with the length of the air-seasoning period following cutting.*

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Recent Reductions in Annual Radial Increments in Dying Scarlet Oaks Related to Rainfall Deficiencies

BY
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R. P. TRUE

MANY SCARLET OAKS (*Quercus coccinea* Muenchh.) died in Pocahontas County, West Virginia, in the summer of 1953. Because the symptoms resembled those of oak wilt, samples were taken from dying trees. Attempts to isolate *Ceratocystis fagacearum* (Bretz) Hunt from these samples failed, and the oak wilt disease was ruled out as the cause of death.

In August 1954 the dying oaks were examined, and where death was prevalent, the site quality was poor. Because the summer and fall of 1953 had been exceptionally dry, it was decided that current dying might have been caused by the 1953 drought. Further investigations were undertaken in 1956 when severe and extensive mortality occurred following the dry summer of 1955. The symptoms shown by the dying oaks, and the known distribution of associated extensive mortality, have been reported previously (Fergus, 1956; Gillespie, 1956; Gillespie and True, 1957).

The study described here was limited to a comparatively small area in which the climate, geology, and soils are quite uniform. The chief purpose is to determine whether a relationship exists between the width of the recent annual rings of dying trees, and the pattern of rainfall recorded in the vicinity. It is also hoped that the information presented will help to explain the extensive dying of affected trees.

Study Areas

In West Virginia the largest known area of dying scarlet oak is situated in Pocahontas County in the mountainous eastern part of the State. An aerial survey by Gillespie (1956) showed that the area was approximately 38 miles long and eight miles wide. Smaller areas occur to the northeast and to the southwest, as well as eastward in Virginia. Dead and dying scarlet oaks are shown in Figure 1.

The West Virginia areas occur predominantly on Ashby and similar shallow soils of medium texture, derived mainly from tilted Devonian shales. The strata have been so folded that in many places the dip of the bedding planes is nearly perpendicular to the surface of the earth. Such soils are subject to excessive drainage from below and are low in nutrients. Poor water-holding capacity and low fertility contribute to

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The authors are Professor of Silviculture and Professor of Plant Pathology, respectively, West Virginia University, Morgantown. Published with the approval of the Director, West Virginia Agricultural Experiment Station, as Scientific Paper No. 570. The authors wish to acknowledge the assistance of Mr. Randall Sharp of Huntersville and the Conservation Commission of West Virginia on whose land the work was carried on.

the low site quality characteristic of these soils.

The forest stands of the area are composed mainly of mixed hardwoods, among which oaks frequently predominate. Eastern white pine (*Pinus strobus* L.) often occurs in considerable abundance. Eastern hemlock (*Tsuga canadensis* (L.) Carr.) may be present although it is never abundant. Only scarlet oak has been seriously affected. A few red oaks (*Quercus rubra* L.) are dying, but species of the white oak (*Q. alba* L.) group have been slightly affected, if at all, in Pocahontas County. White pine and hemlock show no indication of injury.

Four plots were chosen for the study in Pocahontas County. All were within 16 miles of Arbovale, the only weather station in the area from which adequate precipitation records were available. Three of the plots were located on sites where many scarlet oaks were dying, and one plot was located on a site supporting healthy scarlet oaks.

FIGURE 1. *Dead and dying scarlet oaks on a poor site, Seneca State Forest (site index 43).*

The three plots with dying scarlet oaks were named Arbovale, Huntersville, and Seneca, and all the scarlet oaks in these plots were either dead or dying. The control plot contained healthy scarlet oaks, and the most vigorous trees making up the control sample were selected from among a population that included a few showing thin crowns.

The trees measured in each plot were in the dominant or codominant crown class, and showed neither recent suppression nor damage. Control trees were more widely scattered than trees in the other plots. The numbers of trees measured, their ages, and their average site index (tree height in feet at 50 years of age) are given in Table 1.

Organisms Associated with Affected Trees

To supplement limited early culture studies, 94 isolations were attempted in early September, 1956 using a yeast-malt-extract medium. Samples were taken from branches with: (1) live green leaves, (2) leaves showing marginal browning and premature fall discoloration and, (3) dead leaves. Five trees showing typical symptoms, and growing in widely separated localities within the disease area were so sampled. A few injured or dying roots were also cultured. Forty percent of the attempted isolations yielded no organism. Of 27 cultures made from branches with green leaves, 17 were sterile. No recognized pathogenic fungus was found consistently or often among the isolates obtained (Table 2). *Graphium sp.*, the most prevalent fungus, was isolated in only 11 of the 96 cultures. The fungi isolated seem likely to have been secondary invaders.

TABLE 1. Characteristics of scarlet oaks included in each plot.

Name of plot	Number of trees	Condition of trees (September 1956)	Age (Years)	Average site index[1]
Control	7	Completely alive and apparently healthy	32-67	58
Huntersville	13	Partially dead and dying	85-91	50
Arbovale	8	Partially dead and dying	69-92 (One 135)	48
Seneca	9	Partially or completely dead	53-73	43

[1]Height of tree in feet at 50 years of age.

With the thought that earlier droughts might have initiated extensive root dying or root rot, portions of the root systems of 13 widely scattered symptom trees of 1956 were dug early in September, 1956, and examined down to the point at which their diameter was less than ¼ inch. The 100 roots examined were situated near the soil surface for convenience and because such roots would seem likely to be affected by drought. Only 11 roots were found dead at a diameter of ¼ inch. Of these, four had been completely exposed by natural erosion. Only one of the 11 was found dead at ½ inch diameter (Table 3). No study of the root hair zones, mycorrhiza, or small feeder roots was made. All of these might have been severely affected without giving evidence of it in the examinations made. This study shows that the root system of trees dying with advanced symptoms typical of this disturbance were not extensively killed or decayed. Roots of trees suffering from drought are usually the last part of the trees to die (Boyce, 1948).

While the results of the studies reported above do not preclude the possibility that the affected trees were dying as the result of the attack of some pathogenic fungus, they do make that possibility seem remote.

Radial Increment

One increment core was obtained at breast height from each scarlet oak. The width of each annual ring, from 1945 to 1956, was then measured to the nearest tenth of a millimeter. This period was considered long enough to show any increment response the trees might have made to the droughts.

The Seneca plot could not be used because radial increments were so slight that the rings could seldom be identified or measured accurately.

Growth curves for the three plots used, Arbovale, Huntersville, and the control, are presented in Figure 2. The curves provide evidence to substantiate the following:

1. Radial increment dropped sharply after 1949 and the general growth trend continued downward to 1956. The slowing down of growth after 1949 represents a rather abrupt change from the general trend. The trend had been upward for a few years prior to 1949.
2. The difference in radial increment is related to site. The best site (control plot, site index 58) produced the best growth throughout the period. The poorest site (Arbovale,

TABLE 2. Organisms isolated from dying scarlet oaks.

Sources of attempted isolation	Organisms obtained from attempted isolation				
	Fungi		Bacteria	None	
	Graphium	Unidentified or Misc.[1]			Isolations attempted
Branches with green leaves					
Arbovale tree	2	2	0	1	5
Seneca tree	0	1	0	5	6
Huntersville tree	1	2	1	4	8
Watoga tree No. 1	0	1	0	3	4
Watoga tree No. 2	0	0	0	4	4
Totals	3	6	1	17	27
Branches with discolored leaves[2]					
Arbovale tree	0	5	0	2	7
Seneca tree	0	5	0	1	6
Huntersville tree	1	2	1	1	5
Watoga tree No. 1	0	2	0	4	6
Watoga tree No. 2	1	0	0	2	3
Totals	2	14	1	10	27
Branches with dead leaves					
Arbovale tree	1	2	0	2	5
Seneca tree	1	2	0	3	6
Huntersville tree	1	1	0	3	5
Watoga tree No. 1	0	2	0	0	2
Watoga tree No. 2	1	3	0	2	6
Totals	4	10	0	10	24
Roots (injured or dying)					
Seneca tree	1	0	5	0	6
Huntersville tree	1	4	0	0	5
Tree 2 miles south of Seneca State Forest	0	2	2	1	5
Totals	2	6	7	1	16
Grand Totals	11	36	9	38	94

[1]Miscellaneous fungi included some recognized as belonging to genera usually considered to include twig diebacks such as Dothiorella and others not known to cause serious disease. No recognized root rot fungi were isolated.

[2]Discolored leaves showed premature autumn reddening sometimes associated with marginal browning when collected about the first of September, 1956.

site index 48) produced the poorest growth. It is noteworthy that the dying oaks occupied the two poorer sites. All three sites were below the site index average of 66 for oaks on areas in northeastern West Virginia as reported by Trimble and Weitzman (1956).

3. Greatest year-to-year variations in radial increment were found on the best site, and variations were less on the poorer sites.

Possible Droughts

Examinations of the affected area led to the opinion that drought contributed to, or caused, the dying of the scarlet oaks. Therefore, an attempt was made to determine when droughts had occurred and to measure their severity by studying the precipitation records at Arbovale for the years 1949 to 1956. Precipitation at Arbovale averages 39.70 inches per year (U. S. Dept. Agric., 1941).

Defining a drought period is both difficult and arbitrary, but an attempt to do so, as Tannehill (1946) pointed out in his excellent book on drought, should be helpful in evaluating possible drought periods. Such an attempt was neccessary for this work. Parker (1956) includes the following two definitions.

1. British meteorologists define "absolute-drought" as a period of 14 or more consecutive days without rain.
2. The U. S. Weather Bureau defines drought as a period of 21 days or longer when the rainfall is not more than 30 percent of the average for the time and place.

There is a disadvantage in using precipitation as the sole basis for characterizing drought, especially if the U. S. Weather Bureau definition is used, because the availability of soil moisture rather than precipitation alone actually determines effective drought. Some factors, other than precipitation, which influence available soil moisture include intensity of storms, atmospheric humidity, percent of slope, aspect, soil depth, soil texture, and in this instance, position and composition of geologic strata. Although these factors are ignored, the definitions cited by Parker are helpful in determining possible periods of effective drought.

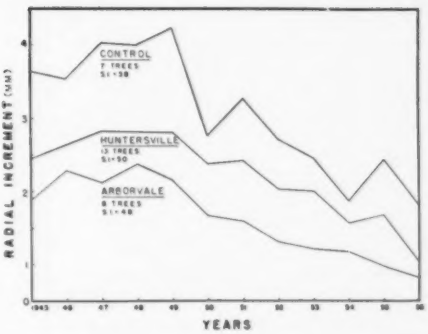

FIGURE 2. *Annual radial increment curves of scarlet oak for the years 1945 to 1956.*

The determination of the years which included periods of drought was attempted

TABLE 3. The condition of surface roots of 13 dying scarlet oaks dug for examination early in September, 1956.[1]

Site	Number of trees examined	Conditions of roots at ¼" diameter		Total number of roots examined
		Number alive	Number dead[2]	
Seneca State Forest	5	18	2	20
Two miles south of Seneca	4	31	3	34
Huntersville	1	14	3	17
Watoga State Forest	3	26	3	29
Totals	13	89	11	100

[1]The upper half of the crown of each tree was dead at the time the roots were examined.

[2]Only 1 of the 11 roots dead at ¼" diameter was also dead at its ½" diameter. Four of the 11 roots dead at ¼" diameter had been completely exposed by erosion some time before examination.

TABLE 4. Monthly precipitation records from Arbovale weather station.[1]

Months	Normal	Year						
		1949	1950	1951	1952	1953	1954	1955
May	3.45	4.41	4.60	3.13	4.59	2.57	3.54	2.24
June	3.71	5.63	3.58	5.82	2.24	6.68	5.46	3.35
July	4.80	4.91	3.77	3.29	3.63	2.39	4.59	1.35
August	3.90	4.84	4.08	1.69	4.26	2.76	6.67	3.18
September	2.62	1.43	7.54	1.80	2.56	1.43	2.24	4.18
October	3.10	3.88	2.26	1.24	0.92	0.85	7.06	1.83

[1]Normal monthly precipitation data from United States Department of Agriculture. 1941. Yearbook of Agriculture. Climate and Man. Washington, D. C. 1248 pp. Monthly precipitation data, 1949 to 1955, from United States Weather Bureau. 1949 to 1955. Climatological data. West Virginia section. The underlined values indicate that the precipitation for that month is about 50 percent or more below normal.

in two ways. The first was to compare monthly precipitation values, as recorded at Arbovale for the summer months, with the normal from 1949 through 1955, as presented in Table 4. The second method was to examine the daily precipitation records during the summer for the same period, as shown in Table 5. Thus droughts occurred in four years out of seven, 1949, 1951, 1953, and 1955, with the worst drought occurring in 1953.

Literature on Ring Width in Relation to Precipitation Periods

Studies on the effect of quantity and time of precipitation upon ring width of forest trees have been made chiefly in the eastern United States, in the Southwest, and in Europe. In a recent work, Tryon *et al.* (1957) reviewed and attempted to analyze literature pertaining to this subject, especially the research studies conducted east of the Mississippi River. For the eastern United States, a definite pattern developed, although variations from the general trend were reported. Where year-to-year variations in ring width occur, width is most closely related to precipitation recorded during or within, the current growing season. In most instances, several years were used as the basis for study, and the effect of any unusual condition on radial increment, such as a late summer drought occurring in any one year and affecting increment the next, might well be masked in the general analysis.

A few workers have studied the effects upon ring width of extremes of precipitation which occur during the latter part of the growing season (Bogue, 1905; Diller, 1935; Robbins, 1921). They found that extremely low rainfall during the latter part of one growing season (a drought) reduced radial increment the following year. Extremely high precipitation during this period, in some instances, resulted in increased radial increment the following year. Beaufait (1956) and Büsgen and Münch (1929) reported that repeated droughts slowed down radial growth, but gave no detailed information.

With these relationships in mind, the ring widths of the scarlet oaks were studied in relation to precipitation in an attempt to learn specifically whether the radial increment was related to (a) early summer precipitation, or (b) deficient or excess precipitation during the late summer and early fall of the previous year. From such a study, a measure of the effect of recurring droughts on the scarlet oaks might be obtained or suggested.

Relationship of Recent Ring Widths to Precipitation Periods in Dying Scarlet Oaks

An attempt to relate the width of annual rings of the scarlet oaks to different precipitation periods was made for the years 1949 to 1956. This interval was used because a general reduction in growth started immediately after 1949 and continued through 1956, and because droughts were known to have occurred within this period. Precipitation periods finally tested statistically include:

Current growing season

May - June[2]
May - July
May - August

Preceding season (storage period)

July - August
July - September

Combination of current and preceding seasons

Current May - June and past July - September

The relationship between variations in width of annual rings and precipitation for each period was tested by means of the correlation coefficient. Differences between years for both radial increment and the precipitation period were used in the test.

The correlation coefficients showing relationship between annual radial increment of each plot and precipitation periods are presented in Table 6. In this table, the figures shown for three of the different precipitation periods were adjusted before testing as is shown by dashed lines in Figure 3.

[2]Precipitation data from the Arbovale weather station were complete except for a portion of the May - June period, 1956. Data used for this period were obtained by interpolation between the figures available at the closest stations in the same geographic area.

TABLE 5. Summary of precipitation figures indicating drought periods for Years 1949, '51, '53, and '55 from Arbovale weather station.[1]

Dates	Days	Precipitation
	Number	*Inches*
1949:		
May 30 - June 15	17	.02
July 19 - August 2	15	.27
August 29 - September 26	29	.59
September 30 - October 9	10	.02
October 11 - October 24	14	.38
Total	85	1.28
1951:		
July 6 - July 24	19	.38
August 14 - August 27	14	.27
October 9 - October 31	23	.42
Total	56	1.07
1953:		
July 8 - July 18	11	0
July 24 - August 3	12	Trace
August 19 - September 4	17	0
September 14 - October 27	44	.11
Total	84	.11
1955:		
May 15 - June 6	21	.19
June 27 - July 7	11	.02
July 9 - July 24	16	.20
July 26 - August 12	18	.30
August 24 - September 2	9	Trace
September 5 - September 22	17	.41
October 15 - October 31	16	.24
Total	108	1.36

[1]Precipitation data from United States Weather Bureau. 1949 to 1955. Climatological data. West Virginia section.

The reason for the adjustment is that the effective drought conditions that occurred in 1949 are inadequately represented by monthly precipitation totals for the July-September period because of the pattern of distribution. A better indication of dry periods in 1949 may be obtained from the daily precipitation amounts presented in Table 5. Elsewhere the amount of precipitation actually received during the period is used to indicate the moisture condition of the soil without regard to its distribution or other contributing factors.

Relationships between ring width in the Huntersville plot and precipitation periods. The relationship between the annual radial increment of the dying scarlet oaks and the precipitation periods is shown for the Huntersville plot in Table 6. The agreement between curves for selected precipitation periods and increment may be observed in Figure 3.

The correlation coefficients from Table 6 indicate best relationships between ring width and rainfall for the precipitation periods of the preceding year. A significant relationship is indicated for the preceding July-September period, and the two adjusted preceding periods, July-August and July-September, are highly significant.

Relationships between increment and current precipitation periods indicate a negative trend which approaches significance when the summer months July, and then August are included in the current precipitation period (Table 6). However, such a relationship is meaningless even though significance is approached because most of the increment would have been completed before July, and certainly before August. Therefore, rainfall in these months should not have a major effect on current annual increment, and certainly not a negative effect on such exceptionally well drained sites.

The correlation coefficients for the current May-June period combined with the preceding July-September period, although significant, are less so than those of the preceding July-September period alone.

Relationship between ring width in the control plot and precipitation periods. The relationship between the annual radial increment of the healthy scarlet oaks on the control plot and the precipitation periods is shown by correlation coefficients in Table 6. The results in general are in agreement with those obtained for the different precipitation periods in the Huntersville plot.

The highest values were obtained for the preceding July-September period, with the adjusted value being the only significant one. Thus, again the preceding July-September precipitation period is most closely related to ring widths.

The yearly responses of the annual radial increment to the preceding July-September precipitation period may be observed in Figure 3. These responses are similar to those of the Huntersville plot but are more pronounced. It is evident here not only that the increment was less following the 1949, 1951, 1953, and 1955 droughts, but that it increased after heavy July-September precipitation in 1950 and 1954. The relationship of past July-September precipitation to ring width is poorer

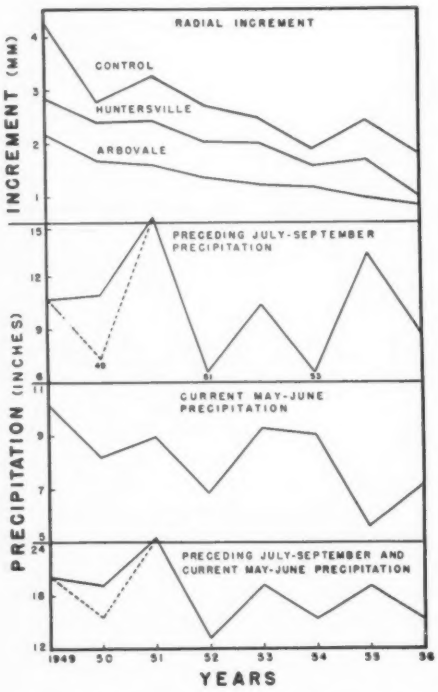

FIGURE 3. *Relationship of annual radial increment of scarlet oak on the three plots with precipitation periods for the years 1949 to 1956. Current and preceding year's precipitation combined and plotted as for the current year.*

TABLE 6. Correlation coefficients showing significant relationships between annual radial increment and precipitation periods (Arbovale station, 1949-1956).

Plot	Precipitation period								
	Current May-June	Current May-July	Current May-Aug.	Preceding July-Aug.	Preceding July-Aug. (Adjusted)[1]	Preceding July-Sept.	Preceding July-Sept. (Adjusted)[1]	Current May-June & preceding July-Sept.	Current May-June & preceding July-Sept. (Adjusted)[1]
Arbovale	.567	.573	.446	—.349	.037	.050	.301	.250	.464
Hunters-ville	—.112	—.513	—.744	.728	.964**	.849*	.898**	.759*	.793*
Control	.0001	—.225	—.414	.264	.673	.584	.782*	.549	.720

[1]Coefficients calculated from adjusted precipitation value for the year 1949 because of the known drought.
*Significant at 5 percent level.
**Significant at 1 percent level.

for the control than the Huntersville plot although the degree of increment response is greater. The reason for this is not understood.

The sharp increment reduction from 1949 to 1950 suggests that some factor, in addition to low soil moisture, also contributed to the change.

Relationship between ring width in the Arbovale plot and precipitation periods. The relationship between annual radial increment of the dying trees on the Arbovale plot and the precipitation periods was tested by correlation coefficients (Table 6). Ring width was not significantly related to any of the precipitation periods. The curve for the Arbovale plot indicates that radial increment decreased each year. Thus there was no increased response associated with high amounts of precipitation for any of the periods. The Arbovale plot had the poorest site quality of any of the plots studied, the site index being 48 as compared to 50 and 58 for the Huntersville and control plots, respectively. Possibly the site was so poor and the trees so low in vigor that they were unable to respond with increased radial increment to more favorable moisture conditions between droughts.

Radial Increment During the 1929-1930 Droughts

After it was shown that dry periods during July to September were associated with reductions in radial increment the following year, the scarlet oaks of the control plot were studied to see if the droughts of 1929 and 1930 also had affected their growth rate. This plot was chosen because all the trees were still alive and the age could be accurately determined and because they had been shown to be the most responsive to differences in amounts of precipitation.

The relationship between radial increment and the preceding July-September precipitation period was compared from 1927 through 1934. The precipitation within this period was much lower in 1929 and 1930 than in any other years, and ring width was much less in 1930 and 1931 than in the other years. Thus low radial increment resulted the year following each drought, a response in agreement with the rest of the study.

The most comprehensive work on the effect of drought on forests of the East is that of McIntyre and Schnur (1936) made in Pennsylvania shortly after the serious 1930 drought which followed the dry season of 1929. Radial increment

studies were included in the investigation. No constant growth response to the drought condition was found for annual radial increment of several species using the precipitation periods they selected. However, ring width of scarlet oak as well as some of the other species they measured was narrow in 1930 and 1931 following the drought conditions recorded for the significant July-September periods of 1929 and 1930.

Response of Radial Increment of Hemlock to Recent Rainfall Deficiencies

Hemlock was occasionally observed growing on sites with dying scarlet oaks or on sites which appeared similar. As hemlock has a shallow root system and is known to be a moist site species, many foresters have expressed surprise that the hemlock did not show signs of injury. Ring widths, from 1945 to 1956, of five hemlocks growing on such a site were measured to test their response to the drought years. Most apparent was the slowing down of growth after 1949, similar to that of the scarlet oaks. However, a close relationship between ring width and the July-September rainfall of the preceding year was not found. This suggests that hemlock, after becoming established on a poor site, is not so sensitive to late summer droughts as is mature scarlet oak.

Discussion and Conclusions

Following observations that scarlet oaks were dying in Pocahontas County, cultures were made from samples and the isolations indicated that neither oak wilt, the first logical suspect, nor any other recognized fungus parasite was causing the trouble. Drought was next considered to be a possible cause of the dying and this investigation was undertaken to determine if radial increment responses could be related to this factor.

The dying occurred on poor sites where soils are characteristically thin, infertile, and are underlain by tilted strata, primarily shales. This combination of soil characteristics and geology results in excessive water seepage and drying of soils during the summer.

Drought periods were determined as nearly as possible from precipitation records of the nearby Arbovale U.S. Weather Bureau station. Dry periods, considered to be droughts, occurred during 1949, 1951, 1953, and 1955, the worst being that of 1953.

Annual radial growth of the dying scarlet oaks was found to have slowed down following the 1949 drought and the growth rate continued intermittently downward through 1956. Thus, decreased growth rate has been associated with successive periods of drought. This response was similar for the healthy scarlet oaks studied on one plot as well as for the dying trees on the other plots.

The annual radial increment of the oaks on all three plots was reduced the year following each of the four droughts. That summer droughts should affect ring width in such a manner is in agreement with the findings of other workers as previously cited. The greatest rate of change in radial increment in response to drought occurred on the two better sites. An explanation for this may be that the oaks, being more responsive on those two sites to both high and low precipitation amounts, reacted more vigorously, producing more marked response both of growth reduction following the drought years and of growth increase following wet years. Trees on poor sites suffered more serious injury, and also seemed unable to make the recovery responses shown by the more vigorous trees on better sites following years of adequate rainfall. Mortality of scarlet oaks was associated with drought which occurred the preceding year. This suggests that the dry weather played an important part in causing these losses. The association seems hardly to have been accidental. It seems more likely that the drought played a causal role of primary importance. Whether ex-

traneous factors also entered the picture or whether drought was the sole cause is not known. It may well be that the complexities of drought situations are at present inadequately understood or narrowly interpreted. This paper has explored the relationship of the losses to rainfall deficiencies in this specific situation. It is hoped and expected that other workers in other areas will include a wider range of possible causal factors in further investigations of drought-related dieback and mortality of trees.

The first summer that large numbers of oaks died was that of 1954, the year following the worst drought within the period studied. In the summer of 1956, following the 1955 drought and presumably also as the cumulative effect of four drought years out of seven, major dying occurred over a wider area and with increasing intensity on sites already affected.

A noticeable characteristic of the disease areas has been the death of small patches or groups of scarlet oaks starting as early as 1953. The margins of these groups of affected trees have expanded from year to year. This manner of spread often characterizes parasitic diseases. However, as the disease seems not to be of parasitic origin, and as major dying followed first the 1953 and then the 1955 drought, the extension is believed to be related to a difference in the effectiveness of droughts on different sites.

This extension of the diseased areas from year to year may be explained by the fact that trees growing on more favorable sites were not at first affected. The cumulative effect of repeated droughts caused the continued dying. This began on the poorest sites, then spread to affect trees on somewhat better adjacent sites within the general area, so that the dying has become not only more severe in areas where it first appeared but also more extensive as time passed.

Age of the trees is another factor which may have a bearing on their decline and death under such conditions of stress. The dying scarlet oaks examined were between 53 and 92 years old, growing on sites well below average productivity. Hepting and Kimmey (1949) stated that decay cull usually causes serious breakup of scarlet oak stands over 80 years old, but that most of the other oak species will pass 150 years without major loss from decay.

The appearance of the stands studied, particularly on the poorest sites, indicated that little more volume increment would be expected from the stand or from the individual trees. Presumably such trees suffer more from drought than trees that are younger and more vigorous.

The results were obtained in this investigation from three small study areas that were not replicated. The difference in degree of increment response on different sites became evident only in the course of this study. The number of trees used in each plot is believed to be adequate because good agreement was found between annual increment of the individuals in each plot.

It is difficult to prove that tree mortality is caused by drought. Conclusive proof does not seem possible at this time. However, the accumulation of information pertinent to the condition should point to, or away from such a cause. In this instance the factors investigated indicate that drought played an important part in causing the death of these trees.

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The Experimental Control of Plant Growth

By Frits W. Went. The Ronald Press, New York. 343 pages. $8.50.

Review by Theodore T. Kozlowski,
University of Massachusetts, Amherst

As an experimentalist Professor Went needs no introduction. His classical investigations on hormonal control of auxin stimulated growth phenomena are well known to plant scientists. Less familiar, perhaps, are his intensive investigations of the last decade on environmental influences on growth, which are summarized in this volume. This is the amazing story of the comprehensive air-conditioned growing rooms of the Earhart Laboratory which allegedly became known as the phytotron because its complex control room resembles that of a cyclotron or synchrotron.

The book comprises 26 chapters presented in 3 sections. The first section of 5 chapters deals with general principles of air-conditioning greenhouses, construction details of the phytotron, sterility maintenance, handling of plants, growing methods and reliability of control. The early chapters provide useful information for anyone with responsibility for greenhouse maintenance. For example, there are good discussions of greenhouse radiation, air circulation and lighting. There is also abundant detail on phytotron construction including floor plans and treatment of engineering problems. Some readers may feel that there is overidentification in this section with minor

details of bookkeeping and handling of plants that were standard operating procedures in the phytotron.

The second section consists of discrete autecological analyses of important plants which were investigated in the phytotron. There are 9 descriptive chapters on the tomato, pea, broad bean, strawberry, miscellaneous cultivated plants, grasses, trees and shrubs, miscellaneous wild plants and chaparall plants. Objectives and methods of approach are outlined and significant results presented with obvious overtones throughout of the importance of thermoperiodicity. Since much of the work summarized here was already published elsewhere it might have been better to omit some of the repetitious details of methodology and further emphasize species comparisons in their reactions to environment. The illustrations showing effects of temperature and time on growth were especially meaningful.

The third section treats in 12 chapters a number of general physiological phenomena including genotypic and phenotypic variability, growth analysis, plant climatology, ecology, germination, photosynthesis, nutrition, and water relations. Included also are chapters on methods for determining water loss, smog, biochemistry and conclusions. Most of the chapters in this section are mature and comprehensive treatments. Some are wanting in completeness and appear to be more or less appended general observations which came out of the experience of operating the phytotron. In the final chapter Professor Went reviews the significance of phytotrons in planning research for the future. He points out that phytotrons provide almost complete physical control over environment and enable simultaneous comparisons of different environments through their wide range of available conditions. Plant scientists have for years used plant materials produced under inadequately controlled conditions. Thus much conflicting data exist which are traceable to experimental conditions or unknown and unappreciated variables. Conclusions have been reached which often are contradictory or tentative. The author believes that henceforth air-conditioning in laboratories, test rooms, artificial light rooms and greenhouses will be mandatory because of the guaranteed increase in research effectiveness. Since phytotrons decrease variability and increase reproducibility less space and fewer plants are required than in conventional greenhouses and this provides justification for diversion of funds toward air-conditioning units. Furthermore, plant response in phytotrons is the same at any time of year. "Air-conditioned greenhouses," concludes the author, "are the most powerful tools at present at our disposal to improve experimental conditions and to minimize the experimental error." The author's views are reinforced by A. H. Hellmers, who contributed one of the chapters. He cites specific examples of the advantages of phytotron testing over field testing. For example, the phytotron reduced the time and expense in selecting plants for erosion control and protection of land after fires.

On the whole the book accomplishes its aims of describing and justifying phytotrons for the future and summarizing the environmental responses of a wide variety of plants. The unseasoned experimentalist can learn much about experimental design and data interpretation through a careful reading of this book. Some readers may consider the title somewhat misleading and will undoubtedly find a few of the chapter titles far too general for the specifics which they contain. A disappointing feature is the brevity of several of the chapters in the last section. The format is appetizing and the 25 plates enhance this readable volume.

Soil Moisture Content and Shortleaf Pine Radial Growth in North Mississippi

BY
D. C. McCLURKIN

TO EXPLORE THE RELATIONSHIP between soil moisture and the radial growth of shortleaf pines, a study was established in 1954 in some 19-year-old plantations in northern Mississippi. The study was designed to determine whether changing tree growth rates closely accompanied changes in soil moisture content, and whether the moisture content in various portions or horizons of the soil profile had different effects on tree growth.

Methods

Three square blocks, each 50 by 50 feet, were laid out on the Tallahatchie Experimental Forest near Oxford, Mississippi, on loessial soils supporting well-stocked plantations of shortleaf pine (*Pinus echinata* Mill.). The plantations had been established in 1935 at a spacing of 6 by 6 feet on abandoned old fields whose furrows and terraces are still visible. Considerable sheet erosion had occurred before the pines were planted, but no gullies had formed. Average tree heights and diameters (Table 1) varied somewhat with soil type.

On one block, the loessial profile contained a weak pan at about 24 inches (Providence soil). On another block, the soil was shallow loess overlying a heavy clay subsoil (Tippah soil). The third block was on a loessial profile that had no impeded drainage (Lexington soil). Understory vegetation was not uniform from place to place. On Block I it was predominantly black locust (*Robinia pseudoacacia*), on Block II mostly green ash (*Fraxinus pennsylvanica*) with some sumac (*Rhus* spp.), and on Block III an even mixture of sweetgum (*Liquidambar styraciflua*) and dogwood (*Cornus* sp.).

Sixteen dominant or codominant trees were selected in each block. On each of these selected trees, two dendrometer stations were established — one on the north side and one on the east—to measure tree radial growth. The dendrometers were read with a dial gauge. During the past few years several investigators, including Daubenmire (1945), have used dial-gauge dendrometers for making precise radial-growth measurements of trees. Brown and coworkers (1947), as well as Stephens and Spurr (1948), used the dendrometer as a tool in growth or thinning studies. Daubenmire and Deters (1947), Fowells (1941), and Jackson (1952) have measured seasonal growth with it. Growth response to moisture was touched on more directly by Dils and Day (1952), who found that 10 to 14 days without rain slackened radial growth in red pine, and concluded that radial growth depended on the presence of surplus soil moisture.

In the center of each block, a stack of 7 fiberglas units was installed to measure

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TABLE 1. Average height, diameter, and basal area of the pines on the study blocks, as measured in December 1954.

Block	Soil type	Average height	D.b.h.	Pine basal area per acre	Understory basal area per acre
		Feet	*Inches*	*Sq. ft.*	*Sq. ft.*
I	Providence	33	5.2	83[1]	31
II	Tippah	31	4.9	121	20
III	Lexington	34	5.4	148	10

[1]Nine trees on Block I were lost to Ips beetles during the summer of 1954.

soil moisture and soil temperature. Units were spaced from just below the surface of the soil to a depth of 42 inches. Four units were placed in the surface foot, and one was placed midway in each foot of the next 3 feet. To calibrate the units, soil moisture samples were taken randomly over the entire 50- by 50-foot block rather than in the usual adjacent 6- by 6-foot plot. Dispersal of the calibration samples over the entire block is a modification of the Area Concept of Reinhart (1953). The purpose in dispersing the calibration samples so widely was to produce a set of calibration curves that would represent the entire study block.

Measurements

Beginning in April 1954, paired readings of soil temperature and moisture and tree radial growth were taken daily (except for weekends) through May 1955, after which they were made twice a week through mid-September of 1955.

A portion of the seasonal growth may have been missed in 1954, since measurements did not begin until April 13. Measurements for the 1955 growing season were taken periodically through the winter months and were resumed on a daily basis in March. Accelerated growth did not begin until early April (Fig. 1).

Rainfall was measured with one recording rain gauge and two non-recording gauges. The recording gauge was approximately a mile from the three study blocks, and the two non-recording gauges were on Blocks I and III. Monthly rainfall values for the duration of the study are shown in Table 2.

At the beginning of the study, undisturbed soil cores were taken on all blocks at the same depths that fiberglas units were installed. These cores were processed in the laboratory for 60 cm. tension and bulk-density values. Disturbed soil samples were taken from the same depths for 15-atmosphere tension values and for texture analyses. The values are recorded in Table 3.

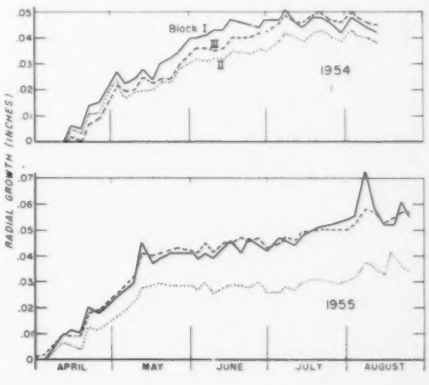

FIGURE 1. *Radial growth curves for shortleaf pine plantations on loessial soils. The points on each curve represent cumulative growth.*

TABLE 2. Rainfall for the April-August period of 1954 and 1955.

Month	Normal	1954	1955
	Inches	*Inches*	*Inches*
April	4.88	3.41	9.25
May	4.38	8.18	2.85
June	4.34	0.67	5.55
July	4.26	2.62	7.50
August	3.61	0.50	1.17
Total	21.47	15.38	26.32

Analysis

As a preliminary step in analysis, the relations between rate of radial growth and selected soil and climatic variables were depicted graphically, with rate of radial growth as the dependent variable and the soil and climatic factors as independent variables. Since day-to-day changes in radial growth were rather small, analysis was based arbitrarily on the field values obtained on Mondays and Thursdays. Growth rate per day then represented the increase in radial measurement since the previous reading divided by the number of days between readings. These values gave average daily rates of growth over short intervals of time.

Upon completion of the graphical analysis, ten of the most promising variables were tested against radial growth rate by multiple regression analysis. The variables included available moisture in different soil horizons, elapsed days of growing season, rainfall, soil temperatures, and interactions between rainfall and season, and between

TABLE 3. Laboratory values for the three blocks.

Block	Depth	Moisture content in three-inch cores, at atmosphere tension— .06	15	Bulk density	Texture[1]
	Inches	*——Inches of water——*			
I	1½	1.24	0.59	1.36	SiCL
	4½	1.30	0.59	1.43	SiCL
	7½	1.34	0.67	1.42	SiCL
	10½	1.34	0.63	1.46	SiCL
	18	1.56	0.77	1.52	SiCL
	30	1.87	1.06	1.46	SiC
	42	1.95	0.88	1.38	SiC
II	1½	1.21	0.26	1.32	SiL
	4½	1.20	0.19	1.46	SiL
	7½	1.17	0.30	1.46	SiL
	10½	1.21	0.46	1.53	SiL
	18	1.07	0.56	1.54	SiCL
	30	1.30	0.56	1.48	CL
	42	1.48	0.89	1.36	C
III	1½	1.22	0.12	1.38	SiL
	4½	1.12	0.18	1.53	SiL
	7½	1.10	0.35	1.46	SiL
	10½	1.14	0.60	1.50	SiCL
	18	1.21	0.55	1.44	SiCL
	30	1.21	0.57	1.43	SiL
	42	1.18	0.47	1.56	SiL

[1]Si = silt; C = clay; L = loam.

temperature and moisture. Since the bark tends to swell after being wetted by rain, one variable—days since rain—was added to account for variations in readings due to this cause.

The graph work indicated that none of the independent variables appeared to dominate the radial growth rate. Therefore, once the variation due to the equation constant was removed from the regression, the independent variables were computed first in the order that would account for the greatest sums of squares each time. Thus with each new reduced set of equations, inspection would indicate which of the remaining variables would account for the greatest sum of squares if calculated next. This shifting of the order of variables in no way affects either the total sum of squares due to regression or the final-error sum of squares, because both these values remain unchanged regardless of the order in which the variables are calculated. In subsequent analyses, different orders of computation of variables also were tried.

Results

The first year of the study, 1954, was extremely dry. Precipitation reached or exceeded normal only in January and May. By late June, the first 4 feet of soil were very nearly at the wilting point. Radial growth ceased early in July (Fig. 1). By November, enough rain had fallen to raise soil moisture above the wilting point, and a little radial growth occurred during the late fall. In interpreting radial growth, no attempt was made to distinguish between cell division and cell enlargement, although late-summer changes in radial dimensions probably were due to cell enlargement.

As can be seen in Figure 1, radial growth for the entire 1954 growing season was only about 0.04 inch. In 1955, radial growth for Blocks I and III was about 0.06 inch, while growth on Block II was less than 0.04 inch.

Although rainfall in 1955 was generally well distributed (Table 2), a deficiency occurred in May and early June. The soil did not reach the wilting point during these months (Figs. 2, 3, and 4), but radial growth virtually stopped until the heavy rains in July.

In the statistical analysis, elapsed days of growing season proved to be one of the variables most closely correlated with growth. Correlation coefficients for this

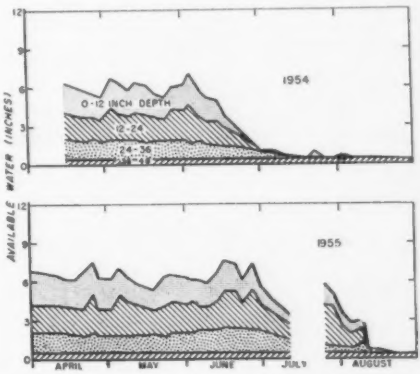

FIGURE 2. *Moisture curves for Block I, showing available moisture in the first 4 feet of soil. Missing data in July 1955 were caused by moisture meter failure.*

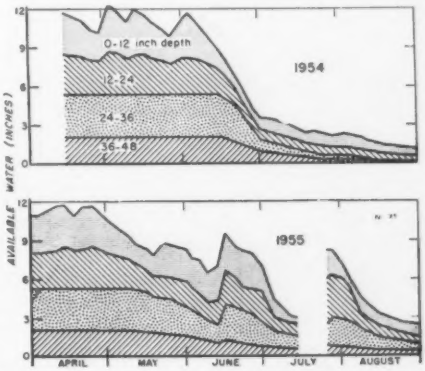

FIGURE 3. *Moisture curves for Block II, showing available moisture in the first 4 feet of soil. Missing data in July 1955 were caused by moisture meter failure.*

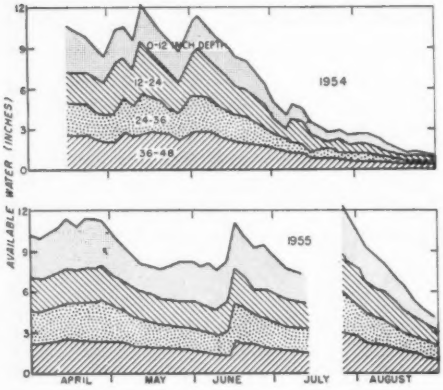

FIGURE 4. *Moisture curves for Block III, showing available moisture in the first 4 feet of soil. Missing data in July 1955 were caused by moisture meter failure.*

variable were —0.42 on Block I, —0.48 on Block II, and —0.38 on Block III. All these values are significant at the 1-percent level. The significance of this variable indicated that for any given set of soil and climatic conditions, the growth rate apparently was more rapid early in the growing season than late. This strong relation was demonstrated on each block by the fact that even after the variation due to all the other factors had been accounted for, passage of days alone still made a significant contribution to the regression sum of squares. No such clear-cut relation independent of the other variables could be shown for soil moisture.

Soil-moisture factors did not perform totally as expected. While there were clearly demonstrable relations between growth and the moisture available in any portion of the soil profile (partly illustrated in Table 4), no small segment of the profile appeared more closely related to growth than did the profile as a whole. There was little difference in effect on growth between moisture in the first 6 inches, the second 6 inches, the first foot, or the second foot. Moisture in the top 4 feet of soil was more closely related to growth variation than moisture in any part of the 4-foot profile. Correlation coefficients for the most important variables appear in Table 4.

In order to study the effect of soil moisture on growth independent of elapsed days of growing season, an analysis was made in which the soil-moisture variables were evaluated first, and the growing-season variable

TABLE 4. Gross or simple correlation coefficients of selected soil-moisture and climatic variables used in the regression analyses.

	Variable	Gross correlation coefficient	"t"
Block I	x_1 (elapsed days of growing season)	—.420	3.99**
	x_5 (available soil moisture in 0–24-inch soil layer)	.379	3.52**
	x_6 (available soil moisture in 0–48-inch soil layer)	.392	3.68**
Block II	x_1 (elapsed days of growing season)	—.482	4.73**
	x_5 (available soil moisture in 0–24-inch soil layer)	.247	2.20*
	x_6 (available soil moisture in 0–48-inch soil layer)	.283	2.55*
Block III	x_1 (elapsed days of growing season)	—.380	3.53**
	x_5 (available soil moisture in 0–24-inch soil layer)	.292	2.62*
	x_6 (available soil moisture in 0–48-inch soil layer)	.298	2.68**

*Significant at the 5-percent level.
**Significant at the 1-percent level.

last. In Block I, the variation attributable to available moisture above the hardpan was not more closely correlated with growth than was the soil water available throughout the entire profile. This was surprising, in view of the paucity of roots encountered in or below the pan during routine soil sampling. After the effect of moisture in the first 4 feet was accounted for, none of the remaining variables in Block I except elapsed days of growing season contributed significantly to regression sum of squares.

Block II has heavy clay subsoil. Here, as in Block I, the growth response was more closely correlated with total available moisture than with any other soil or climatic variables. Numerous soil cores had been removed from the block during the course of laboratory analysis and calibration. Many of the cores from the heavy clay layers contained tree roots. The clay, though tough and plastic, seemingly had not seriously impeded root penetration.

Block III is well drained. Trees here grew as fast as on Block I, and appreciably faster than on Block II (Fig. 1). As on Blocks I and II, when the variation attributable to the available moisture in the first 4 feet of soil was evaluated, only a variable involving elapsed days of growing season—either singly or in combination with moisture or temperature—still made a significant contribution to the regression sum of squares.

Comparisons between radial growth curves (Fig. 1) and soil moisture curves (Figs. 2, 3, and 4) indicate that radial growth rate varies with available soil moisture, and tends to drop off during prolonged periods of rapid soil moisture depletion. For example, during the drying period of May 3 to 20, 1954, growth was only a few thousandths of an inch. Then after a brief spurt following the rain at the end of the month, growth again slowed down as the soil resumed drying. Again in 1955, all trees slowed during May as the soil-moisture content declined steadily.

There is a statistical correlation—mostly inseparable—between elapsed days of growing season, rainfall, available soil moisture (any horizon), soil temperature, and interaction combinations of these variables as they affect growth rate (the dependent variable). Although these factors made significant contributions to the regression sum of squares, usually at the 1-percent level if evaluated immediately after the equation constant, there still remained an appreciable variation in daily growth rate that is unexplained by any and all of the variables tested.

Summary

This study was designed to determine the day-to-day and season-to-season influence of soil moisture and climatic variables upon radial growth of shortleaf pine in northern Mississippi.

Three study blocks were established in 19-year-old shortleaf pine plantations on representative loessial soils.

Tree radial growth and associated soil-moisture and climatic factors were measured frequently during the growing seasons of 1954 and 1955.

The strongest correlations found were those between radial growth and elapsed days of growing season, and between growth and available moisture in the entire 4 feet of the soil profile. The variable, elapsed days of growing season, indicated that growth rate would not be the same for all parts of the growing season even under similar combinations of soil moisture and climatic factors which might be repeated throughout the growing season. Appreciably more growth variation was described by the moisture changes in the entire 4 feet of soil than by moisture changes in any fraction thereof, whether in the surface foot or otherwise.

Despite highly significant correlations between radial growth and the moisture and climatic variables tested, there is still considerable unexplained variation in daily growth rates.

Radial growth tended to drop off sharply

during periods of rapid soil-moisture depletion.

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Directory of Workers in the Economics of Forestry

The Division of Forest Economics and Policy of the Society of American Foresters is compiling a directory of people in the United States and Canada who are working currently in the general area of the economics of forestry. The utility of the directory in facilitating contacts among workers with common interests, in opening up lines of communication for workers in fringe areas, and as a fund of personal data depends in large measure upon its inclusiveness. If your present work or interest treats the economics of production, harvesting, processing, marketing or consumption of forest products and services from any viewpoint, please write to Professor A. C. Worrell, 360 Prospect Street, New Haven 11, Connecticut, for a data sheet.

Prediction of Acorn Crops

By
LESLIE W. GYSEL

LONG RANGE PREDICTIONS of the size of acorn crops of the red oak group may be possible because of the relatively long maturation period of the acorns. After the flowers are fertilized the acorns gradually develop over a period of 16 to 18 months. Predictions of crops of the white oak group may be of shorter duration because the period of acorn development is 5 to 6 months. To explore possible methods of predicting the size of acorn crops, a series of observations was made over a period of 6 years on the flowers, immature, and mature acorns of black oak (*Quercus velutina* Lamarck), red oak (*Quercus rubra* DuRoi), and white oak (*Quercus alba* L.) in southern Michigan. Results of these observations are summarized in this paper and the possibilities of predicting acorn crops are discussed.

Predictions of the size of acorn crops may be useful in both forest and game management. For example, the time of cutting of oak for the shelterwood or clear-cut harvest methods designed to provide seedling reproduction might be determined months before the cut if the size of the acorn crop were known. In game management the size of a future acorn crop may be a factor in determining hunting regulations for squirrels, and possibly for deer in some areas.

Methods

Initial data and ideas were obtained by tagging and observing flowers and immature acorns on the lower branches of isolated trees and stand border trees for 3 years. Later, tests were made to determine the possibility of using binoculars and spotting scopes for observing and counting flowers and immature acorns on the entire crown of mature trees. After a method of sampling was devised, numerous observations and counts of flowers and immature acorns were made on sample trees at different seasons in six different areas for 3 years. The size of the mature acorn crops from these trees was indicated by the number of acorns collected in seed traps with a surface area of 10.9 square feet.[1]

Results

Sampling procedure. On small trees 40 or 50 feet in height, flowers and acorns can often be counted with binoculars. Most of the trees sampled in this study were from 60 to 90 feet in height. To observe flowers and acorns at these distances a series of tests was made with a spotting scope with eyepieces to provide a power range of 20×, 30×, and 60× with a 60 mm. objective. The scope was set as near to the tree as possible for a convenient angle of sight. The average distance for a scope setting for a 75-foot tree was 80 feet, which made a sighting distance of 109 feet to the top of the tree. Flowers and immature acorns could generally be seen

[1]Gysel, L. W. 1956. Measurement of acorn crops. Forest Science 2: 305-313.

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best with a 30× eyepiece at this distance.

A useful system of sampling devised for this study consisted of recording the number of flowers or acorns on each twig in various sample areas throughout the tree crown. All live twigs of the outer branches having growth of the current season were included in the sample areas for the flower and early immature acorn counts on trees of the red oak and white oak groups. All vigorous twigs having stem growth of the previous season were included in the sample areas for the second-year acorn counts on trees of the red oak group. A minimum of 20 twigs was counted for each tree. The counts for each tree were summarized by determining the number of flowers or acorns per branch.

The relationship of the actual number of flowers and acorns of black oak to the scope count was determined by observing one group of collected twigs with flowers and a second group of twigs with immature second-year acorns at 110 feet with the scope and then making an actual count on each twig. The results for both groups were approximately the same. Of the total number of flowers according to the check count, 53 percent were counted with the scope and of the total number of immature acorns 51 percent were counted with the scope. Most of the flowers and acorns missed in the scope counts were on the side of the stem opposite the line of sight or were closely appressed to the stem-like buds. The average difference between the check count and the observed count per twig for both flowers and immature acorns was 0.58; 87 percent of the counts were either correct or in error by one flower or acorn. Similar results were obtained from counts of red oak and white oak twigs. The scope counts can therefore be used to indicate the number of flowers or acorns produced and may be used to estimate major differences or changes in the seed crops. On individual trees, scope counts may be influenced by the size and position of acorns or flowers and by the amount of leaf or male flower cover at the time of counting.

In relating the number of acorns per branch to the size of the total crop, as estimated from seed trap counts, one other variable must be considered—the density of acorn-producing branches in the crown. This was difficult to measure; however, it was noted that the number of branches producing acorns per unit area of most border and open-grown trees was relatively high in comparison with the number of branches on interior trees. Therefore, tree positions are given in the tables to aid in evaluating the relationships between flower and immature acorn counts and the number of mature acorns in the seed traps.

Flowers and acorns of the red oak group. The flowers of this group can best be observed when they are full grown and before the leaves are completely developed. The flowers of red oak are relatively prominent and are often easily seen with a spotting scope (Fig. 1A). The flowers of black oak are often less prominent than those of red oak because they grow close to the stem on many trees and are similar in color to the stem (Fig. 1B). The partly expanded leaves and the male catkins which develop with the flowers sometimes limit the number of twigs and flowers that can be observed, especially on short twigs with closely spaced leaves; however, enough flowers can generally be seen to determine the trend of flower production on most trees.

Twigs can be easily seen during the winter and early spring months for spotting scope counts of the small immature acorns which remain about the same in size during this period (Fig. 2A, B).

Spotting scope counts of flowers and subsequent counts of immature acorns were made on a group of sample trees listed in Table 1. A large number of the flowers on most of the trees observed during May and June 1956 developed into immature acorns according to the October count. An April count of the small immature acorns indicated no discernible losses. According to counts of the nearly mature acorns made in August, 1957, changes appeared to be

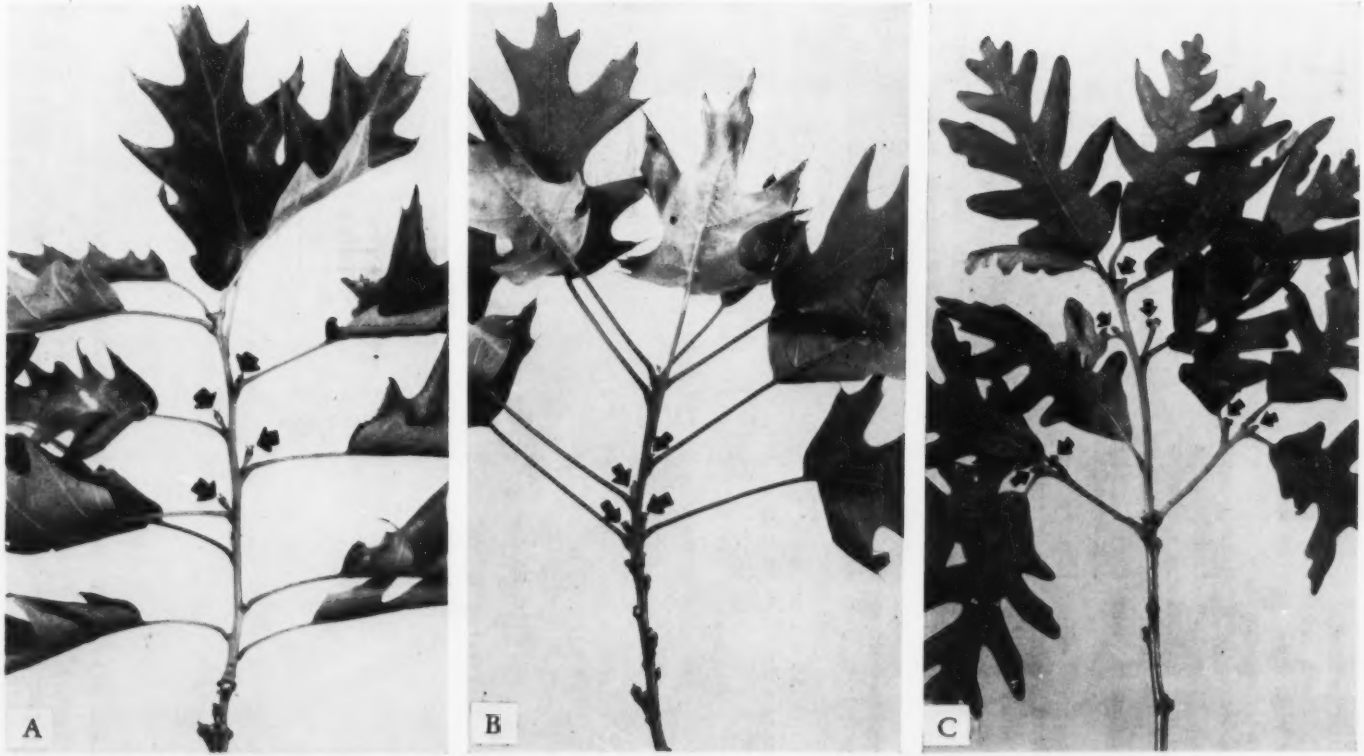

FIGURE 1. *Flowers of three species of oak are indicated by arrows: A.—Red oak collected May 22, 1957. Immature acorns that originated during the previous season are on the twig below the leaves. B.—Black oak collected May 22, 1957. Immature acorns are also on this twig below the leaves. C.—White oak collected June 2, 1957.*

relatively minor on most of the trees.

To interpret the relationship between the number of acorns per trap and the count of flowers and immature acorns per branch in Table 1, the tree position must be considered. The number of branches per unit area over the seed trap was greatest on trees grown in the open; the number of branches on south-facing border trees was greater than on the north-facing border trees. For 9 of the 12 trees there is a relatively close relationship between the number of flowers and immature acorns per branch and the number of acorns per trap. Exceptions are black oak 8 and red oak 1 on which there were losses of immature acorns. The flower count on black oak 7 was obviously erroneous.

The counts of immature acorns in Figure 3 were made in April before the leaves developed. In 1955 the number of acorns per trap was relatively high in relation to the number of immature acorns per branch. It is possible to assume from this that a large proportion of the immature acorns that were tallied in April formed mature acorns. In 1956 and 1957 the number of acorns per trap was relatively low in relation to the spring counts. In 1957 counts of immature acorns were also made in early August; these were considerably lower than the April counts on the same trees indicating a large loss of acorns during the summer months. In one area the average number of immature black oak acorns counted in April was 1.6; an average count from the same trees in August was 0.3 and the average number of mature acorns per seed trap was 7.

Flowers and immature acorns of the white oak group. The leaves of white oak which are approximately one-half to full size during the period when the flowers are ex-

FIGURE 2. *Immature acorns of two species of oak collected April 23, 1957, just before the beginning of the second growing season. Acorns are indicated by arrows: A.—Red oak. B.—Black oak.*

TABLE 1. Number of flowers and immature acorns per branch from spotting scope counts and the number of acorns per seed trap.

Species	Tree Number	Tree Position	Flowers per branch May-June '56	Immature acorns per branch Oct. '56	Apr. '57	Aug. '57	Acorns per trap Sept.–Nov. '57
Black Oak	1	North-facing border	1.4	1.7	2.2	1.6	18
	2	Do	0.0	0.1	0.8	0.4	4
	3	Do	1.1	1.1	1.1	0.9	8
	4	South-facing border	2.0	1.5	2.5	3.0	87
	5	Do	1.8	1.1	1.6	2.0	40
	6	Do	1.2	1.2	2.1	1.6	42
	7	Open	0.4	2.0	2.3	3.0	206
	8	Do	1.6	1.1	1.7	0.1	23
Red Oak	1	South-facing border	1.4	0.4	0.7	0.1	3
	2	Do	0.0	0.0	0.0	0.0	0
	3	Do	0.4	0.0	0.0	0.0	1
	4	Open	1.1	1.3	1.4	1.6	32
	5	Do	—	2.0	—	2.0	31

tended sometimes limited the number of flowers that could be counted (Fig. 1C). Also, counts were more difficult on some trees on which the leaves grew in dense groups than on trees on which the leaves were widely separated; however, enough flowers could generally be counted to make an estimate of the number of flowers per branch on most trees.

The acorn production of white oak is often poor in lower Michigan; therefore, the majority of observations will probably be similar to those made in 1956 (Table 2). The absence or small number of flowers was reflected in the small number of mature acorns in the August count and also in the small number of mature acorns per trap.

The large white oak acorn crop in 1957 (Table 2) was indicated by a relatively large number of flowers and immature acorns per branch. For some trees the August count of immature acorns was higher than the floral count; this was probably due to the fact that groups of acorns developed from flower clusters that could be counted only as a single flower.

Discussion

Sometimes the earliest possible prediction of acorn crops may be of greatest value to foresters and wildlife managers. A count of the number of flowers could be the basis of an early prediction. If no flowers were produced the acorn crop of species of the red oak group would be a failure 16 to 18 months later; the crop failure of species of the white oak group would occur 5 to 6 months later during the same year. If flowers were numerous, a large crop of acorns might develop during some years but during other years losses of flowers might occur during some phases of the period of development. Wright[2] noted that heavy flowering of oaks may not indicate heavy fruiting. During some years in Michigan oak flowers may be killed by frost. Therefore, if the prediction of the size of acorn crops is made on the basis of the average number of flowers per branch, subsequent observations should be made to

[2]Wright, J. W. 1953. Notes on flowering and fruiting of Northeastern trees. Northeast. Forest Expt. Sta. Paper No. 60.

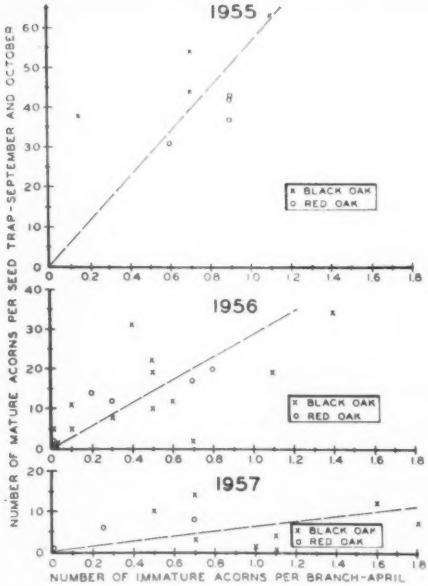

FIGURE 3. *The relationship of spotting scope counts made in April to the number of mature acorns collected in seed traps from dominant and codominant trees in closed stands. The trend lines were drawn freehand.*

check the trend of acorn development.

It was assumed during the course of this study that spring counts of immature acorns of the red oak group would probably be an accurate indication of the mature crop because the acorns at this stage and during subsequent stages of development appeared to be least affected by environmental conditions that might drastically reduce the crop before maturity. This assumption was true for most of the trees analyzed in Table 1 and apparently true for the 1955 data in Figure 3 although an August count was not made in the latter case. It was not true, however, for the counts made in 1957 (Fig. 3); a count of the acorns per branch in August indicated a sharp reduction in the crop during the summer. This apparently occurred on many trees in 1956 also, although the reduction was not as great. The general relationship between the spring counts of immature acorns and the seed trap counts for each of the three years in Figure 3 is different. Therefore if predictions are made on the basis of winter or spring counts of immature acorns, it will be necessary to make subsequent checks to de-

TABLE 2. Number of flowers and immature acorns per branch and the number of acorns per seed trap for white oak.

Tree number	Tree position	Flowers per branch—June	Acorns per branch—Aug.	Acorns per trap Sept.–Nov.
		1956		
1 to 10	Open	0.2[1]	0.1[1]	5[1]
		1957		
1	North–facing border	1.3	1.9	86
2	Do	1.3	2.4	145
3	Open	—	3.5	585
4	Do	2.3	1.7	353
5	Do	—	0.4	11
1	West–facing border	1.1	0.8	98
2	Do	0.9	1.6	210
3	Do	1.1	0.7	31
4	Open	1.3	1.8	172
5	Do	1.3	1.3	170

[1]An average of counts from 10 trees.

termine the trend of development each year.

In the case of the white oak group, immature acorns are sometimes difficult to to see until they are almost full size, about one month before the acorns fall. This limits the possibilities of predicting the size of the crops following the floral stage.

To estimate the acorn crop of a stand, it is suggested that counts of flowers and immature acorns be made on at least 15 dominant and codominant oak of each species in a stand, a number based on an analysis of estimates of mature acorn crops.[3] An average of these counts should indicate the potential size of the acorn crop. In general, counts of flowers or immature acorns less than 1.0 acorn per branch by a spotting scope may indicate acorn crops that could be classed as medium to poor; counts from 1.0 to 2.0 may be medium to good, and 2.0 or more may be very good.

The first observations of tagged flowers and immature acorns on easily accessible low limbs provided data concerning the development of these plant parts. It did not appear practical, however, to use these data for the prediction of acorn crops on entire trees because acorn production on low limbs was often less than that on the upper parts of the trees. In addition tagging and counting flowers and immature acorns was a time-consuming operation.

Summary and Conclusions

An attempt was made to determine the possibilities of predicting the size of acorn crops by counting the number of flowers or immature acorns. On small trees 40 to 50 feet in height, flowers and acorns can often be counted with binoculars. In this study, all counts were made on taller trees with a spotting scope, generally with a 30× eyepiece. The number of flowers or immature acorns on each twig in various sample areas throughout the trees was counted and the average number per branch determined for each tree. The scope counts can be used to indicate the number of flowers or immature acorns produced and may be used to estimate major differences or changes in the seed crop.

If no flowers are produced, the acorn crop of species of the red oak group will be a failure 16 to 18 months later; the crop failure of species of white oak will occur during the same year. If flowers are produced, acorns may or may not develop from them; therefore, subsequent checks should be made to determine the trend of development.

If immature acorns of species of the red oak group develop, twigs can be easily seen for making counts during the winter or early spring after the first growing season before the leaves are completely formed; this count may indicate the size of the mature crop; however, losses of the partly mature acorns may occur during the summer months; therefore additional observations should be made.

For species of the white oak group, the most complete observations of immature acorns can generally be made when the immature acorns are almost full size.

There appears to be no infallible method for an early prediction of the size of mature acorn crops if flowers and immature acorns are produced. Early predictions can indicate the potential size of a crop; however, the actual size can be determined only by later observations and check counts.

[3]Gysel, L. W. *Op. Cit.*

Influence of Land Use and Forest Condition On Soil Freezing and Snow Depth

BY
ROBERT S. PIERCE
HOWARD W. LULL
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THE RELATION OF LAND USE to the occurrence, depths, persistence, and type of frost has been studied by many investigators. Overall results are well known: frost is much more common in open land than under forest stands; and when frost does occur in forest soils, it usually does not penetrate so deeply. This is mostly because forest soils are warmer. Compared to open-land soils, their insulating cover of vegetation and litter restricts loss of summer-stored heat and thereby inhibits freezing. This cover also slows warming in the spring so that frost in forest soils may persist longer than in open-land soils.

The influence of forest cover on frost has an important supplemental effect; for where severe soil freezing occurs, soil permeability is reduced. Rainfall or water from melting snow is then forced to flow over the frozen soil as surface runoff; it reaches the stream quickly and thereby contributes to flood peaks. These relationships were well recognized by early workers. More recently, the beneficial protection offered by forest cover was further acknowledged when gross differences in frost types were found to be associated with open-land and forest-soil freezing. The frost type most common to open lands—concrete frost—restricted infiltration and promoted surface runoff, whereas frost types most commonly found in forest soils did not have this effect.

Most of the early investigations of soil freezing were limited to a few frost observations on a few land-use conditions; these often provided comparative data for such extremes as heavy forest growth and exposed open sites. Little information is available on winter-long frost conditions for different kinds of open-land use such as pasture, hayland, and bare cultivated land at a number of widely sparated locations. Nor have the effects of forest type, age, and condition on frost been given systematic study over a wide range of conditions and locations. The purpose of this study was to obtain information of this kind in the Northeast.

This paper reports results from a two-winter study (1950-52) designed to obtain information about frost conditions in 18 different land-use and forest conditions at six locations from Maine to Pennsylvania. Average concrete frost depths and concrete frost frequency are described and compared as they relate to the various land-

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use and forest conditions. Among the several types of frost, concrete frost alone is emphasized because of its singular effect of promoting runoff during spring thaws and rainfalls. In conjunction with periodic frost measurements, measurements of snow depth were taken and also related to land use and forest conditions.

Previous Work

Some of the first observations of frost penetration in soils were made while comparing depths of freezing under forest stands as opposed to cultivated lands. Hough (1877) reported that early European investigators found much deeper frost in open fields than in the forest. Zon (1927) cited work by Schubert in Germany in 1900, which indicated that soils under forest stands may remain unfrozen while those in open fields froze to considerable depths. When freezing did occur in the forest soils, they froze to one-half or less than three-quarters the depth of those in the open. A similar relationship was noted by Pearson (1911), who found that frost depth under stands of western yellow pine was one-half that in open grass-covered areas. Similar results were observed by Jaenicke and Foerster (1915) in Arizona. Scholz (1938) reported comparable findings from a study in Wisconsin: frost penetrated to a depth of 4 inches in a hardwood woodlot and to a depth of 10 inches in a bluegrass sod pasture.

Diebold (1938) found in New York that soils in bare fields froze to depths of 30 inches, while soils under hardwood forests, abandoned meadows, and a pasture remained unfrozen. Goodell (1939) found average frost depths in southern Illinois of 5.5 inches in a cornfield and 1.5 inches in a pasture, but no frost in an oak-hickory forest.

Kienholz (1940) compared frost depths in soils in Connecticut under several forest conditions having different species, age, size, and stocking, and also under grass sod and plowed fields. He observed that soils of the open non-forest sites froze to depths twice that in the forest.

In Wisconsin, Atkinson and Bay (1940) found that frost penetrated twice as deep under bluegrass sod and five times as deep under plowed fields as in a protected woodlot. Post and Dreibelbis (1942) reported that when soils under winter wheat and pasture in Ohio froze to maximum depths of 10 inches and 4 inches respectively, soils under a deciduous woodland remained unfrozen. Salisbury (1939), in Great Britain, found that frost penetrated to 8.5 centimeters under bare sandy loam, to 3.5 centimeters under grass, and not at all under undisturbed hazel brush. In central California under similar cover types (i.e., bare, grass, and brush) Anderson (1947) found average maximum frost depths of 2.56, 0.46 and 0.0 inches for the three types respectively.

Various reasons have been offered as to why frost penetration in forest soils is not so deep as in open fields: winter soil and air temperatures are generally warmer in the forest than in the open; deciduous forests may accumulate a more uniform snow depth through reduction in drifting and thereby have a more uniform depth of the protective insulating blanket that snow provides; and litter and humus produced by forests are generally a better insulator against loss of heat than is the thinner covering of organic materials produced by vegetation in open areas.

The effect of forest type upon the depth-duration of frost in soils has been studied to a limited degree. Kienholz (1940) observed that frost penetrated slightly deeper in hardwood stands than in soils under white pine, but that in the spring the frost persisted longer in the pine stand than in the hardwood.

Belotelkin (1941) reported less frost penetration and a shorter frost period in soils under northern hardwood forests than under red spruce stands. He attributed this to the greater insulating effect of hardwood litter and humus and the deeper snow layers that result from less snow interception.

Soils in a black spruce swamp were frozen slightly deeper than those in red spruce stands, and the frost persisted in the black spruce for one month or more longer.

Several rather distinct structural forms of soil frost have been observed. Post and Dreibelbis (1942) described three types: *concrete*—consisting of many very thin ice lenses, small crystals, and extremely dense structure; *honeycomb*—having loose porous structure that allows free vapor movement; and *stalactite*—characterized by small, vertical icicles that join heaved surface particles to the main soil below. An additional type of frost structure was recognized by Hale (1950), which he called *granular*. This was characterized by scattered granules of ice binding the litter and "F" (fermentation) layers of the humus.

These various structural forms of frost are caused by a complex of factors such as texture, structure, and porosity of mineral soil; soil moisture content; rate and duration of freezing; type and depth of humus and litter; and depth of snow. Lassen and Munns (1947) noted that humus depth was one of the critical factors associated with the formation of concrete frost.

An up-to-date discussion of soil freezing in relation to land use is given by Colman (1953). Papers by Anderson (1947) and Bullard (1954) also contain excellent reviews of the literature.

The effect of land use and forest condition on snow depth has also been well summarized by Colman (1953) and need not be restated here. Suffice it to say that complicated relationships are involved: generally, open lands, where snow is directly exposed to wind and solar radiation, will have shallowest snow depths; deciduous stands, which slow wind movement, provide some shade, and yet do not intercept significant amounts of snow, tend to have the deepest snow covers; intermediate are conifer stands, which tend to balance losses due to interception with gains resulting from reduced wind velocities and from reduction in melt-rates by heavy shading.

FIGURE 1. *Location of frost study areas in the Northeast.*

Methods of Study

Experimental Areas

Frost and snow depth measurements were taken in east-central Maine, east-central New Hampshire, northern New York, southern New York, northwestern Massachusetts, and northeastern Pennsylvania (Fig. 1) during the winters of 1950-51 and 1951-52. At five of these six areas, data were obtained on or close to experimental forests, the exception being the southern New York area where work was centered around Deposit, N. Y. Throughout this report, these areas will be designated as shown in Table 1.

At each area 12 to 17 land-use conditions were selected for study, covering a range of 18 conditions in all. Four of the conditions consisted of open land: bare cultivated [1],[1] hayland [2], good pasture [3], and poor pasture [4]; three consisted of abandoned or clear-cut land [5, 6, 7]; two conditions were coniferous plantations one 12 to 18 years old [8], the

[1]Numbers in brackets refer to land-use and forest condition numbers given in table 2.

TABLE 1. Experimental areas used in Northeastern frost study.

Area	Location	Elevation in feet	Forest cover			Soils
			Pole & sawtimber	Plantation	Reproduction	
Penobscot	Penobscot Exptl. Forest Bangor, Maine	160	Northern hardwoods, spruce-fir	Red pine	Beech, alder, maple, aspen	Loams: stony loam to clay loam
Paul Smiths	Paul Smiths Exptl. Forest Paul Smiths, N. Y.	1,760	Northern hardwoods	Red pine, spruce-fir	Maple, cherry, willow, aspen	Sands: loamy sand to sandy loam
Bartlett	Bartlett Exptl. Forest Bartlett, N. H.	630	Northern hardwoods, white and red pine	White pine	Aspen, cherry	Sands: loamy sand to sandy loam
Hopkins	Hopkins Exptl. Forest Williamstown, Mass.	920	Northern hardwoods, red oak, hemlock	White pine	Aspen, oak, cherry	Loams: stony loam to sandy loam
Deposit	Deposit, N. Y.	1,600	Northern hardwoods, hemlock	Red pine	Beech, maple	Loams: stony silt loam, silt loam, stony clay loam
Pocono	Pocono Exptl. Forest Gouldsboro, Pa.	1,820	Northern hardwoods, hemlock	Scotch pine	Aspen	Loams: stony loam, fine sandy loam, loam

other 30 to 35 years of age [9]; three were either in coniferous or hardwood poletimber of different degrees of stocking [10, 11, 12]; the remaining six conditions consisted of coniferous, hardwood, or mixed sawtimber in various degrees of stocking and use.

Within each of the six areas the land-use and forest conditions selected for study were contained generally within an area of 10 to 15 square miles. Almost all plots were located on well-drained or moderately well-drained soils and on slopes of sufficient steepness to insure surface drainage; slopes were generally 10 percent or less and variable in aspect. A description and area allocation of the various land-use conditions are given in Table 2.

Field Measurements

At each land-use condition within each area two plots were laid out, each 50 x 50 feet.

TABLE 2. Land-use conditions for each of the six study areas.

Land-use condition	Penobscot	Paul Smiths	Bartlett	Hopkins	Deposit	Pocono
1. *Bare cultivated:* cultivated annually in the spring.	X	X	X	X	X	X
2. *Hayland:* permanent hay at least 1 year.	X	X	X	X	X	X
3. *Good pasture:* good sod covering, no bald spots.	X	X	X	X	X	X
4. *Poor pasture:* sparse sod, many bald spots, scattered weeds and brush.	X	X	....	X	X	....
5. *Hardwood reproduction:* not exceeding 10 feet in height, abandoned farmland.	X	X	X	X	X	X
6. *Hardwood reproduction:* not exceeding 10 feet in height, clear-cut area.	X	X	X	....	....	....
7. *Clear-cut:* within past 5 years, no reproduction.	X	X	X	X	....	X
8. *Coniferous plantation:* 12-18 years, well stocked, 71-100 percent crown closure.	X	X	....	X	X	X
9. *Coniferous plantation:* 30-35 years, well stocked, 71-100 percent crown closure.	X	X	X	X	....	....
10. *Hardwood poletimber:* well stocked, 71-100 percent crown closure.	....	X	X	X	X	X
11. *Hardwood poletimber:* poorly stocked, crown closure less than 40 per cent.	X	....	....	X	....	X
12. *Coniferous poletimber:* well stocked, 71-100 percent crown closure.	X	X	X	X	X	X
13. *Hardwood sawtimber:* undisturbed, well stocked.	....	X	X	X	X	X
14. *Hardwood sawtimber:* well stocked, logged within past 5 years, moderate selective cut.	....	X	X	X	X	X
15. *Hardwood sawtimber:* grazed, well stocked.	X	X	....	....	X	....
16. *Coniferous sawtimber:* undisturbed, well stocked, 71-100 percent crown closure.	X	X	X	X	X	X
17. *Coniferous sawtimber:* well stocked, logged within past 5 years, moderate selective cut.	X	X	X	X	X	....
18. *Coniferous-hardwood sawtimber:* undisturbed, well stocked, 71-100 percent crown closure.	....	X	X	....	....	....

TABLE 3. Weather during period of freezing at each area.

Area	Duration of freezing period[1]		Mean daily temperature		Accumulated temperature deficiency[2]		Precipitation	
	1950–51	1951–52	1950-51	1951-52	1950-51	1951-52	1950-51	1951-52
			°F.	°F.	°F.	°F.	Inches	Inches
Penobscot	Dec 13–Mar 26	Dec 9–Mar 30	23.3	21.6	1000	1278	11.97	14.21
Paul Smiths	Dec 9–Mar 27	Dec 10–Mar 31	20.4	20.6	1316	1429	8.29	7.39
Bartlett	Dec 14–Mar 27	Nov. 18–Mar 30	24.8	25.6	869	961	11.20	16.61
Hopkins	Dec 12–Mar 27	Dec 11–Mar 29	26.7	25.5	685	860	14.18	12.42
Deposit	Dec 9–Apr 6	Dec 10–Mar 29	21.7	22.9	1306	1355	11.19	14.43
Pocono	Dec 10–Mar 27	Dec 11–Mar 29	24.2	23.5	958	1003	12.32	13.80

[1]Period of below-freezing temperatures. This period begins with the first daily mean temperature (average of maximum and minimum temperatures) below freezing that is followed by 2 or more consecutive days below freezing and extends to the last consecutive date with below-freezing temperature. Intermittent periods of 1 or 2 days above freezing were included in this period.

[2]Sum of degree-days below 32°F. during the freezing period. The number of degree days for any one day of below-freezing temperature is calculated by subtracting the daily mean from 32°F.; i.e., 22°F. equals 10 degree-days.

Twice weekly, frost and snow data were recorded from observations and measurements taken at two points systematically selected in each plot. Frost type, frost depth in each soil layer, litter and humus depths, snow depth, and snow-moisture content (for the second winter only) were recorded. Depth of concrete frost was measured to a maximum of 10 inches—considered to be the maximum depth of excavation permissible in accordance with time and labor available. (Greater depths were recorded as 10+ inches of frost.) Measurements were taken at the plots about 35 times during each of the two winter seasons.

Daily precipitation and maximum and minimum temperatures were measured at a weather station in each of the six areas. Stations were located in the center of the areas or not more than five miles from the plots.

Opposing effects on climate of decreasing latitude and increasing elevation tended to minimize temperature differences. Thus, despite a range in latitude of 270 miles, periods of below-freezing temperature at the six areas tended to coincide (Table 3). Paul Smiths, second in elevation and latitude, had the coldest weather during the two winters, followed by Deposit, located in the Catskills, and Penobscot, the most northerly area. Pocono, in the mountains of northeastern Pennsylvania, had lower mean temperatures and a greater accumulated temperature deficiency than either Hopkins or Bartlett, 99 and 194 miles farther north, respectively.

Hopkins received the greatest amount of precipitation during the first winter, 14.18 inches; during the second winter Bartlett ranked first with 16.61 inches. Paul Smiths had the least amount recorded each winter, 8.29 and 7.39 inches. Precipitation for the other areas was rather uniform (Table 3).

Since the climatic stations of this study were temporary, it cannot be determined whether temperature and precipitation during the 1950-51 and 1951-52 seasons were normal. However, there were no large discrepancies between the average temperature and precipitation measurements given in Table 3 and the normal isograms prepared by Kincer (1941).

Analysis of Data

Although four types of frost were observed and noted in the field (concrete, honeycomb, stalactite, and granular) only concrete frost will be discussed in this paper. Frost data were analyzed to derive average depth of concrete frost; frequency of occurrence; and accumulated depth, a value expressing both depth and frequency. (Henceforth, the term *frost* as used in this paper refers to concrete frost.) An average snow depth was computed.

The analyses of depth frequency in relation to accumulated depth were used to preserve, as far as possible, frost values that had hydrologic meaning. Thus, frost depth, as calculated, is not an average depth for all observations (which would have little physical significance) but rather the average depth for those times that frost occurred. Similarly, frequency, unless noted otherwise, is expressed mainly as a percentage of observations when concrete frost occurred at all four points of measurement at each condition, rather than at one or more points; for it is under conditions of wide rather than sporadic distribution that concrete frost particularly influences surface runoff.

Average frost depth. For each date of measurement an average frost depth was calculated for each condition in each area. These values were then summed up for each winter and an average value of frost depth was calculated by dividing by the total number of frost occurrences for each condition in each area during the winter. For all conditions the number of occurrences in one winter ranged from none to 36.

Frost depths for both winters were then averaged and tabulated into a series of 19 logical comparisons of frost depth in open land and forest, hayland and pasture, hardwood and conifer, and the like. Significance of differences was tested by the method described by Snedecor (1946) for orthogonal sets of comparisons. An average depth for each condition for all areas was also calculated.

Percentage of frost occurrence. As a measure of frequency, the percentage of frost occurrence during each winter was calculated for each land-use condition of each area. To permit valid comparisons between conditions in each area the percentages were calculated from a common base, the number of observations between the first and last recording of frost in the area. Thus the percentage equaled the total number of days on which frost was observed, divided by the total number of observations during the frost period, times 100. For all areas, 27 to 38 observations were taken each winter between first and last appearance of frost. Percentages were calculated for those observations when concrete frost appeared at all 4 of the points examined and at 1 of 4, 2 of 4, and 3 of the 4 points. An average percentage for each condition for all areas was also calculated for the 4-point occurrences.

Accumulated frost depth. To integrate the frost-depth and frequency values, a third statistic was calculated: accumulated depth. This value was the product of the average frost depth for each winter's record, times the number of days of frost, times the percentage of observations for which frost was recorded at all four sampling points. As observations were taken twice weekly, the number of frost days was estimated: if frost occurred on two consecutive observations, days between were counted as frost days; frost-free periods were considered to extend from the date of the first recording of no frost to the date of its next recording. (Because of this element of estimation, the actual number of frost occurrences rather than the number of frost days was preferable for deriving the percentage of frost occurrence described above.)

Accumulated depths were calculated for each condition within each area and for each condition for all areas.

Average snow depth. Average snow depths were calculated by dividing the sum of the

depths measured by the number of measurements. To compare the effects of forest types and conditions between areas, ratios of snow depths for each forest condition to average depths in open-land conditions [1, 2, 3, 4] were computed.

Results

Frost and Snow Occurrence by Areas and Major Conditions

Ranges of average frost depth, percentage occurrence, accumulated depth, and average snow depths by areas and major land-use conditions are given in Table 4.

Average frost depth. Frost depths ranged from 0.0 to 7.2 inches. In all six areas, hardwood stands had the lowest values, and three of the six areas had minimum values in the well-stocked hardwood sawtimber condition [13]. Maximum values without exception occurred in open land; all but one were in the bare cultivated condition [1].

Varying by areas, average frost penetration in forest land [10, 12, 13, 16] of 0 to 5 inches was about one-half the 3- to 7-inch penetration in open land [1, 2, 3, 4]. This is an underestimate in the open land to the extent that frost penetrated below 10 inches, the maximum depth measured. In this and subsequent comparisons the Bartlett area has notably less frost in the forest condition. This is probably due to the

TABLE 4. Ranges of frost depth, percentage occurrence, accumulated depth, and snow depth by areas and major conditions.

Area	All conditions	Open [1, 2, 3, 4]	Forest [10, 12, 13, 16]	Conifer [12, 16]	Hardwood [10, 13]
		Average frost depth, in inches			
Penobscot	3.3 – 7.2	5.6 – 7.2	3.3 – 4.3[2]	3.3 – 4.3	— —
Paul Smiths	1.0 – 7.1	5.2 – 7.1	1.0 – 5.2	2.7 – 5.2	1.0 – 1.8
Bartlett	.0 – 7.2	6.4 – 7.2[1]	.0 – 1.7	1.4 – 1.7	.0 – 1.2
Hopkins	1.5 – 5.7	2.6 – 5.7	2.2 – 2.9	2.9 – 3.3	2.2 – 2.3
Deposit	1.8 – 5.6	3.4 – 5.6	1.8 – 4.8	4.6 – 4.8	1.8 – 1.8
Pocono	1.6 – 4.8	3.7 – 4.8[1]	1.6 – 2.4	1.7 – 2.4	1.6 – 2.1
		OCCURRENCE (PERCENT)			
Penobscot	7 – 83	69 – 83	37 – 49[2]	37 – 49	— —
Paul Smiths	10 – 76	72 – 76	20 – 46	38 – 48	20 – 24
Bartlett	0 – 100	90 – 100[1]	0 – 1	0 – 1	0 – 0
Hopkins	12 – 75	31 – 75	15 – 54	44 – 54	15 – 19
Deposit	24 – 70	43 – 70	26 – 64	64 – 64	26 – 30
Pocono	15 – 82	74 – 82[1]	15 – 42	25 – 42	15 – 32
		ACCUMULATED FROST DEPTH (INCHES)			
Penobscot	10 – 603	446 – 603	89 – 177[2]	89 – 177	— —
Paul Smiths	3 – 535	364 – 535	8 – 245	78 – 245	8 – 18
Bartlett	0 – 948	743 – 948[1]	0 – 0	0 – 0	0 – 0
Hopkins	6 – 453	47 – 453	14 – 141	101 – 141	14 – 22
Deposit	24 – 377	126 – 377	24 – 344	312 – 344	24 – 38
Pocono	9 – 417	282 – 417[1]	9 – 68	20 – 68	9 – 35
		SNOW DEPTH (INCHES)			
Penobscot	1.7 – 6.8	1.7 – 4.0	4.9 – 6.3[2]	4.9 – 6.3	— —
Paul Smiths	3.5 –12.0	3.5 – 6.1	6.2 –10.6	6.2 – 6.8	9.1 –10.6
Bartlett	10.2 –24.9	10.2 –12.9[1]	18.6 –24.0	18.6 –19.8	22.7 –24.0
Hopkins	2.1 – 4.8	2.1 – 3.7	2.3 – 4.8	2.3 – 2.6	4.3 – 4.8
Deposit	2.2 – 6.6	2.5 – 4.1	2.6 – 6.6	2.6 – 4.8	5.7 – 6.6
Pocono	1.0 – 4.4	1.0 – 2.1[1]	2.1 – 3.7	2.1 – 3.7	3.0 – 3.1

[1]For conditions 1, 2, and 3 only.
[2]For conditions 12 and 16 only.

greater snow accumulation, which averaged—as will be noted later—two to five times deeper than snow in the other areas. While this served to insulate the forest soil from frost, it had less effect on the open-land soils because they were well frozen before snow accumulated to any depth.

Just as frost penetration in forest stands was about one-half as deep as in the open, so frost penetration in hardwood stands averaged roughly about one-half that in conifer stands, 1.5 and 3 inches respectively.

These frost depths are averages for those times in which frost occurred; they do not reflect frequency. The relation of depth to frequency, expressed as percentage occurrence, is close: as will be noted, their correlation coefficient is 0.876.

Percentage occurrence. The percentage of observations in which frost was observed under the different conditions varied from 0 to 100 percent at Bartlett to 24 to 70 percent at Deposit. Again, most maximum and minimum values were for open land and hardwoods, respectively. Frost was observed more than twice as frequently in open land as in forest land, averaging 70 and 28 percent of the observations, respectively. Likewise frost occurred in conifer stands about twice as often as in hardwood stands, averaging roughly 39 and 19 percent. Thus, the 2:1 ratios exhibited in frost-depth penetration also were evident in frost occurrence. As noted previously, the above percentages are based on appearance of concrete frost at all four points examined at each condition.

Accumulated depth. The accumulated depth on open land was found to be 5.6 times that in the forest, averaging 412 compared to 74 inch-days. Conifer values compared to hardwood give about an 8 to 1 ratio, averaging 136 and 16 inch-days.

Snow depth. Generally, greater accumulation occurred in the forest than in the open though differences were smaller for the three southerly areas. Average depths for open and forest lands were 4.1 and 8.0 inches respectively.

More snow accumulated in hardwood stands than in conifer stands, probably because of less interception. Except for the Penobscot area, snow depths averaged about 2.7 inches or 29 percent deeper in the hardwood stands.

Frost Depth Comparisons by Conditions Within Areas

Nineteen comparisons of average concrete frost depths by areas are given in Table 5; comparisons are made between land uses, hardwood and conifer stands, age classes, and effects of forest grazing and logging. These values represent an average of the measured frost depths; they do not reflect frequency of frost occurrence. As observed, however, average frost depth and percentage of occurrence have a correlation coefficient of 0.876. Therefore the comparisons in Table 4 may be interpreted specifically in terms of frost depth and generically in terms of both depth and frequency.

Land uses. The first two comparisons demonstrate again the greater frost depths recorded on the open lands. In the first comparison between open land and undisturbed well-stocked hardwood and conifer pole and sawtimber stands, differences were highly significant for all six areas: average frost depths were about twice as great in the open, 5.3 to 2.8 inches. Comparison 2, involving open lands and forest reproduction, gave substantially the same results: frost depths averaging 5.6 to 2.9 inches.

Frost depths on the bare cultivated plots were significantly greater than depths in the open grassland at Penobscot, Hopkins, and Pocono. For four of the six areas, the difference was less than 1 inch of frost. Frost depth differences between hayland and pasture (comparison 4) were even smaller: five of the six areas had differences of 0.7 inch or less. Of the three significant differences, two showed greater frost depths in the hayland, and the other had the greater depth in the pasture. Comparison 5, between good and poor pastures,

TABLE 5. Comparative depths of concrete frost.

Comparisons	Concrete frost depths						Conditions compared
	Penobscot	Paul Smiths	Bartlett	Hopkins	Deposit	Pocono	
	Inches						*Number*
1. Open land	6.3**	6.4**	6.7**	3.5**	4.8**	4.2**	1,2,3,4
Forest land	3.8	3.3	1.4	2.7	3.2	2.1	10,12,13,16
2. Open land	6.3**	6.4**	6.8**	3.5**	4.8**	....	1,2,3,4
Forest reproduction	4.0	2.2	2.8	2.2	3.2	....	5,6,8
3. Bare cultivated	7.2**	7.1	7.2	5.7**	5.1	4.8**	1
Grass land	6.0	6.2	6.4	2.7	4.7	4.0	2,3,4
4. Hayland	5.6	5.2*	6.4	2.9	5.2*	4.2*	2
Pasture	6.2	6.7	6.4	2.6	4.5	3.7	3,4
5. Good pasture	6.4	6.7	....	2.7	5.6**	....	3
Poor pasture	6.1	6.8	....	2.6	3.4	....	4
6. Hardwood poletimber	....	1.8**	1.2	2.2	1.8**	1.6**	10
Conifer poletimber	....	5.2	1.4	2.9	4.6	2.4	12
7. Hardwood sawtimber	....	1.0**	.0**	2.3*	1.8**	2.1	13
Conifer sawtimber	....	2.7	1.7	3.3	4.8	1.7	16
8. Hardwood reproduction, abandoned farm	3.3*	1.3	3.4	....	....	....	5
Hardwood reproduction, clear-cut	4.2	1.0	2.2	....	....	....	6
9. Hardwood reproduction, clear-cut	4.2	1.0**	2.2	....	....	....	6
No hardwood reproduction, clear-cut	4.0	3.4	3.2	....	....	....	7
10. Hardwood reproduction	....	1.2	2.8**	2.4	3.0**	....	5,6
Hardwood poletimber	....	1.8	1.2	2.2	1.8	....	10
11. Hardwood reproduction	....	1.2	2.8**	2.4	3.0**	....	5,6
Hardwood sawtimber	....	1.0	.0	2.3	1.8	....	13
12. Hardwood poletimber	....	1.8	1.2	2.2	1.8	1.6	10
Hardwood sawtimber	....	1.0	.0	2.3	1.8	2.1	13
13. Conifer plantation, 12–18 years	4.5	3.8	....	2.1	....	....	8
Conifer plantation, 30-35 years	4.2	3.4	....	2.5	....	....	9
14. Conifer plantation	4.5	3.8*	....	2.1**	3.3**	3.6**	8
Conifer poletimber	4.3	5.2	....	2.9	4.6	2.4	12
15. Conifer plantation	4.5**	3.8*	....	2.1**	3.3**	3.6**	8
Conifer sawtimber	3.3	2.7	....	3.3	4.8	1.7	16
16. Conifer poletimber	4.3*	5.2**	1.4	2.9	4.6	2.4*	12
Conifer sawtimber	3.3	2.7	1.7	3.3	4.8	1.7	16
17. Hardwood grazed sawtimber	....	2.8**	....	....	2.0	....	15
Hardwood ungrazed sawtimber	....	1.0	....	....	1.8	....	13
18. Hardwood logged sawtimber	....	1.7	.8	1.5*	2.1	1.9	14
Hardwood unlogged sawtimber.	....	1.0	.0	2.3	1.8	2.1	13
19. Conifer logged sawtimber	3.6	2.1	2.5	2.7	3.8*	....	17
Conifer unlogged sawtimber	3.3	2.7	1.7	3.3	4.8	....	16

* Significant at 5-percent level.
** Significant at 1-percent level.

showed very little difference for three of the four areas studied, whereas at Deposit frost depth in the good pasture was significantly greater, 5.6 vs. 3.4 inches.

Hardwood vs. conifer. The next two tests, 6 and 7, involve ten comparisons of frost depths under hardwood and conifer stands. Of these, seven (four of the five sawtimber-stand comparisons and three of the five poletimber stand comparisons) gave significantly greater depths in the conifer stands. Significant differences average about 2

inches more frost under the conifer stands.

Hardwood conditions. The next five comparisons, 8 to 12, reveal no consistent differences between frost depths in hardwood reproduction on abandoned farmland and clear-cut areas; but they show, for two of four areas, frost significantly deeper (1.2 to 2.8 inches) under hardwood reproduction than under hardwood poletimber and sawtimber. There were no significant differences in frost depths between these latter two categories.

Conifer conditions. Comparisons 13 to 16 for conifers were somewhat inconclusive. Differences between frost depths of the two plantations were not significant. Frost depths were significantly shallower in the conifer plantation than in the poletimber stand at three of five areas, while the reverse condition occurred at Pocono. The plantation-sawtimber comparisons showed significantly shallower depths in the plantations at 2 of 5 areas, and significantly deeper at the other three. Differences were all in the neighborhood of 1 to 2 inches depth. At three of the six areas there were no significant differences in frost penetration of sawtimber and poletimber stands. Significantly greater differences of 1.0, 2.5, and 0.7 inches were calculated for Penobscot, Paul Smiths, and Pocono poletimber stands, respectively.

Grazing and logging. Grazed hardwood stands had a significantly greater frost depth at one of two areas, as shown by comparison 17. As can be noted in comparisons 18 and 19, light logging had little effect on frost depth.

Frost Frequency and Its Relation to Frost Depth

The percentages of observations in which frost occurred at all 4 points examined at the study plots, and at 1 of 4, 2 of 4, and 3 of 4 points are given in Table 6. For open-land conditions, appearance of concrete frost is associated with wide distribution: on an average concrete frost was observed at all 4 points of measurement 73 percent of the time and 86 percent of the time at 1 of the 4 points. The situation is quite different for forest conditions: comparable values (excluding the Bartlett area) are 35 vs. 56 percent. Thus, under forest conditions, while concrete frost was recorded at 1 of 4 points in slightly more than one-half of the observations, it was widely distributed only one-third of the time.

Comparable percentages for conifer and hardwood conditions are 46 vs. 70 percent and 23 vs. 41 percent, and for hardwood reproduction and conifer plantations, 34 vs. 51 percent and 43 vs. 72 percent. Widespread concrete frost, therefore, occurred in hardwood stands one-half as frequently as in conifer stands, with hardwood reproduction midway in frequency. There was little difference in frost occurrence between conifer timber and plantations.

Frost occurrence-frost depth. A close relationship might be expected between frost occurrence and frost depth, that is, the higher the incidence of frost found in an area the greater the frost penetration. To test this, average frost depth for the 2 years of record for each condition in each area was plotted against its percentage occurrence at all 4 points (Fig. 2). The relationship is linear and such that an increase in 1 inch of frost depth is associated with a 13-percent increase in percentage occurrence. The correlation coefficient of 0.876 is highly significant.

Average Frost Occurrence by Conditions For All Areas

Average frost depth, percentage occurrence, and accumulated depth for all areas are given in Table 7. Using accumulated depth as the best indicator of frost conditions, land-use conditions were ranked in descending order of incidence. On this basis, land-use conditions fall into three groups, with 10 to 27, 51 to 158, and 307 to 553 inch-days of frost. In terms of average frost depths these groups span frost depths of 1.2 to 2.5, 2.5 to 3.5, and 4.7 to 6.2 inches, respectively. Percentages of occurrence overlap slightly, ranging for the

three groups in the same order—12 to 20, 17 to 44, and 57 to 80 percent.

Values in the table, of course, are not of the same order of precision. As can be noted, values for conditions 1, 2, 3, 5, 12, and 16 are averages for all six areas, whereas condition 18 was represented in only two areas. Because of these variations —plus the fact that the averages are for widely scattered areas and have no location relevance—the table is of more value for relative comparisons by groupings than by individual conditions.

The three clear-cut divisions in Table 7, averaging 412, 101, and 18 inch-days, invite classification. The first division, *high frost intensity*, is associated with open-land conditions, and the specific use to which the land is put apparently has little influence on the amount of frost. An *intermediate intensity* follows; it is correlated with conditions exemplified by brushy land and conifer stands. The third class, *low frost intensity*, is associated with hardwood cover. Roughly, frost intensity in open lands was 4 times greater than that on brush lands

TABLE 6. Percentage of frost occurrence by major land use and frost distribution.

Land use condition	Number of points at which frost was observed	Percentage of occurrences					
		Penobscot	Paul Smiths	Bartlett	Hopkins	Deposit	Pocono
Open land [1,2,3,4]	4	69	74	96	77	55	71
	3	74	77	97	81	65	73
	2	79	82	100	90	70	79
	1	81	82	100	95	75	80
Forest [10,12,13,16]	4	....	32	0	33	46	28
	3	....	39	0	39	55	35
	2	....	44	1	49	61	44
	1	....	51	3	57	68	49
Conifer forest [12,16]	4	43	43	1	49	64	33
	3	51	55	1	54	73	39
	2	56	63	2	62	81	50
	1	66	73	6	69	87	55
Hardwood forest [10,13]	4	....	22	0	17	28	24
	3	....	23	0	24	37	32
	2	....	26	1	35	41	38
	1	....	29	1	44	49	43
Hardwood reproduction [5,6]	4	36	12	10	31	44	46
	3	52	13	13	38	51	46
	2	71	15	26	45	51	49
	1	77	21	44	54	54	49
Conifer plantation [8,9]	4	42	51	0	14	54	54
	3	54	68	0	19	73	55
	2	71	82	0	31	83	62
	1	78	85	0	39	90	66

and conifer sites, and 23 times greater than frost under hardwood stands.

In this classification, apparently neither size nor stocking of coniferous timber had any great influence on frost intensity; all coniferous sites fell in the intermediate classification. For the hardwood stands, size class seemed to have effect in that hardwood reproduction was classified as intermediate whereas poletimber and sawtimber stands had low frost intensity.

Light logging had little influence on the intensity classification of the hardwood or conifer stands. Grazing, on the other hand, tended to give greater frost intensity, grazed hardwood sawtimber ranking first in the intermediate condition.

Snow Depth Comparisons by Conditions Within Areas

There was considerable variation in average snow depth for each area, ranging from 18.8 inches at Bartlett and 7.8 inches at Paul Smiths to 4.4 inches at Penobscot and 3.2, 3.8, and 2.8 inches at Hopkins, Deposit, and Pocono respectively.

In order to compare differences in snow depth between conditions for all areas, ratios of average snow depth for each condition were computed, using as a base the average snow depth for the four open-land conditions (Table 8). In 63 comparisons, 55 had ratios greater than 1.0 indicating greater snow depths in the forest and brush lands than in the open, four had equal ra-

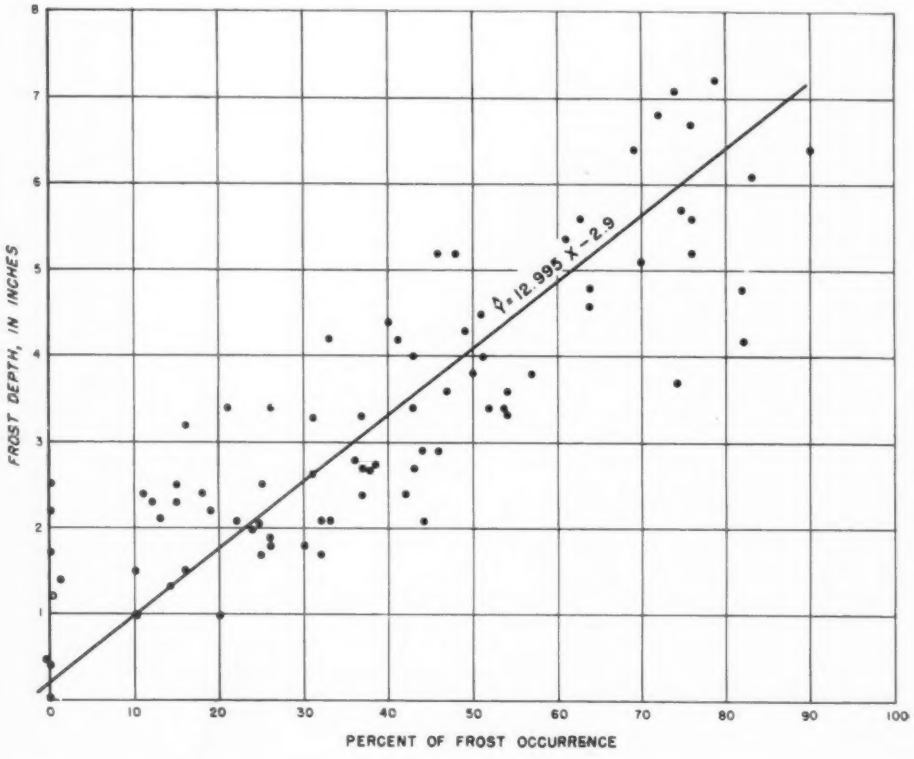

FIGURE 2. *The relationship between frost depth and percentage of frost occurrence.*

TABLE 7. Average frost depth, occurrence, and accumulated depths for all areas.

Land-use condition	Frost			Areas represented
	Depth	Percentage occurrence	Accumulated depth	
HIGH FROST INTENSITY	*Inches*	*Percent*	*Inch-days*	*No.*
1. Bare cultivated	6.2	80	553	6
3. Good pasture	5.2	69	408	6
2. Hayland	4.9	71	382	6
4. Poor pasture	4.7	57	307	4
INTERMEDIATE FROST INTENSITY				
15. Hardwood sawtimber (grazed)	3.4	41	158	3
8. Coniferous plantation (12–18 years)	3.5	44	151	5
12. Coniferous poletimber (well stocked)	3.5	41	150	6
16. Coniferous sawtimber (well stocked)	2.9	36	112	6
17. Coniferous sawtimber (logged)	2.9	33	95	5
7. Clear-cut, no reproduction	3.4	32	74	5
9. Coniferous plantation (30–35 years)	2.6	25	68	4
6. Hardwood reproduction (clear-cut area)	2.5	17	52	3
5. Hardwood reproduction (abandoned farm)	2.6	39	51	6
LOW FROST INTENSITY				
11. Hardwood poletimber (poorly stocked)	2.5	20	27	3
14. Hardwood sawtimber (logged)	1.6	20	21	5
10. Hardwood poletimber (well stocked)	1.7	18	17	5
13. Hardwood sawtimber (well stocked)	1.4	19	16	5
18. Coniferous-hardwood sawtimber (well stocked)	1.2	12	10	2

tios, while four comparisons with ratios from 0.6 to 0.9 indicated the opposite condition. Seven of the eight having ratios equal to or less than 1.0 were located in the three most southerly areas. Generally, as indicated in Table 8, forested conditions in these areas had less influence on snow depth than did conditions in the three northerly areas.

The overall effect of cover can be noted from the means. Hardwood forest and hardwood reproduction averaged 1.75 times more snow depth than was measured in the open. The coniferous forest influence, with a ratio of 1.5, was somewhat less. Lesser accumulation of snow in the open than in the forested sites may be due to the greater rate of melt in the open resulting from its greater exposure; lesser accumulation of snow in the conifer sites than in hardwood may be due to the greater interception of snow by evergreen foliage.

Discussion

The relative incidence, depth, and persistence of concrete frost in the various land-use and forest conditions studied provide new insights into forest-frost relationships and responsible forest influences, and suggest broad management practices for minimizing frost.

Frost in Field and Forest

Previous studies have indicated that frost is deeper in open land than in the forest,

TABLE 8. Ratios of snow depth in the forest to snow depth in the open.

Land-use condition	Penobscot	Paul Smiths	Bartlett	Hopkins	Deposit	Pocono	Mean
8. Coniferous plantation (12–18 years)	1.9	1.7	....	1.1	0.7	2.0	....
9. Coniferous plantation (30–35 years)	1.6	2.2	1.6	1.0	....	....	....
12. Coniferous poletimber (well stocked)	1.8	1.3	1.7	1.0	1.5	2.3	....
17. Coniferous sawtimber (logged)	0.6	2.1	1.5	1.1	1.1	....	....
16. Coniferous sawtimber (well stocked)	2.2	1.5	1.6	0.9	0.8	1.3	....
18. Coniferous-hardwood sawtimber (well stocked)	....	1.8	1.4	....	....	....	....
Mean	1.6	1.8	1.6	1.0	1.0	1.9	1.5
5. Hardwood reproduction (poorly stocked)	2.4	1.9	1.5	1.7	1.2	2.0	....
6. Hardwood reproduction (clear-cut)	2.0	2.6	1.9	....	....	....	....
7. Clear-cut, no reproduction	1.9	1.9	1.9	1.3	....	1.2	....
Mean	2.1	2.1	1.8	1.5	1.2	1.6	1.7
11. Hardwood poletimber (poorly stocked)	2.2	....	....	1.6	....	2.2	....
10. Hardwood poletimber (well stocked)	....	2.0	1.9	1.8	1.7	1.9	....
15. Hardwood sawtimber (grazed)	1.4	1.3	....	....	1.0	....	....
14. Hardwood sawtimber (logged)	....	1.8	2.1	1.3	1.0	2.8	....
13. Hardwood sawtimber (well stocked)	....	2.3	2.0	1.7	2.0	1.9	....
Mean	1.8	1.8	2.0	1.6	1.4	2.2	1.8
Ratio base; average snow depth for open-land conditions (inches)	2.8	4.6	12.0	2.6	3.3	1.6	

but there has been little information as to the frequency of its appearance or the extent of its distribuiton. Results of this study —which dealt only with concrete frost— corroborate previous findings that frost is deeper in the open: frost penetrated to depths of 3 to 7 inches in open lands and 0 to 5 inches in forest lands. Of equal importance are results dealing with frequency of occurrence and distribution. Frost was observed over twice as often in open as in forest land. When frost was present in open land it was observed at all points of measurement about three-fourths of the time. However, frost in the forest occurred at all points only about one-third of the time. These differences are undoubtedly of such magnitude as to influence strongly the disposition of snow melt and spring rainfalls.

Also of significance is the fact that frost was observed 31 percent of the time in forest stands and, as previously stated, occurred at all points of measurement about one-third of the time. Therefore, it is more frequent and widespread in the forest and may have a greater effect on spring runoff than was heretofore realized.

Finally, the wide divergence between frost conditions in conifer and hardwood stands should be emphasized. Frost depth in hardwood stands averaged about one-half of that in conifer stands; frost occurred twice as often in conifer stands as in hardwood stands; and when it did occur it was found at all points 46 per cent of the time in conifer stands as compared to 23 percent of the time in hardwood stands. Thus the range of frost intensity between conifer and hardwood conditions is about the same as between open-land and forest conditions.

Forest Influences

In large measure the factors responsible for differences in frost between the various land-use and forest conditions are differences in organic-matter content, in compaction, in micro-climate, in vegetative cover, and in snow.

Bare cultivated fields have the least or-

ganic matter, are the most compacted and have the least vegetation to act as a buffer against temperature extremes. And they had the most frost. Following them, in respect to these same factors and to frost, come hayland and pasture. Forests, with a blanket of organic matter covering the soil, with porous uncompacted soil, and with a high, heavy stand of vegetation to ameliorate extreme temperatures (forests are warmer than open land in the winter) had the least concrete freezing of all conditions.

Within the forest cover itself, the factor accounting for the most clear-cut difference in frost conditions was the type of forest. Thus significantly greater depths and higher occurrences of concrete soil freezing were found under conifers than under hardwoods. One reason for this is that hardwoods have a deeper protective snow blanket; their crowns are less dense and intercept less of the snow that falls. A second reason for this difference is less obvious and more speculative; it lies with the differences in types of litter and humus found under the two kinds of stands.

Hardwood litter is composed of layer after layer of matted leaves which typically cover a crumbly humus composed of a mixture of organic matter with mineral soil. The matted litter apparently provides good insulation against heat loss from the soil. In this litter, frost crystals may be present but in most cases they are not continuous within or between leaf layers. In the crumbly humus beneath, when frost is present, it rarely forms the concrete type.

The litter of coniferous stands is composed chiefly of needles, which are not layered and thus probably do not offer so much protection against heat loss as the hardwood leaf layers. Also, the humus under the needle litter is not generally incorporated with the mineral soil but lies as a sharply defined layer above it. Concrete frost often forms in the underlying mineral soil before it does in the humus above.

Considerable reduction in frost penetration was noted in abandoned farm lands allowed to seed to natural hardwood reproduction. As vegetative characteristics of hardwood brush in winter favor snow accumulation, the amount of frost under these conditions would be less than under grass or cultivated fields with shallower snow depths. Then too the advent and growth of vegetation with its accompanying addition of humus to the soil mitigates still further against concrete freezing.

To the extent that logging and grazing reduce the depth of the humus layers, compact the soil, and reduce the insulating effect of the stand, they tend to favor the occurrence of concrete freezing. But the picture is complicated by the fact that many stand disturbances may reduce the crown canopy and favor greater snow accumulation and less frost. Thus, without careful study of the variables and adequate sampling of a number of stands it is not possible to define fully the relative effects of stand disturbances.

Forest Watershed Management

What is the significance of these findings to forest watershed management in the Northeast? From this study we can only draw inferences. Continued watershed research may in time provide answers in their final form; namely, as to the effects of frost on streamflow.

Proceeding from the argument that concrete frost is not desirable since it promotes surface runoff during periods of potential flooding from spring thaws and rainfalls, results of this study suggest several management measures. For instance, the greater prevalence of frost in open lands suggests that abandoned lands should be given fire protection and permitted to revert to hardwood brush or planted to hardwoods as soon as possible. Planting of conifers cannot be recommended as a means of ameliorating soil freezing. Where frost control is a primary management objective, established conifer plantations should be thinned to provide deeper snow accumulations, and invasions of hardwoods should be encouraged. Likewise, any forest treatment

or use that reduces litter and humus depth should be discouraged; i.e., fire, grazing, and heavy cutting. Light logging, on the other hand, apparently has little effect on frost. These suggestions lend further support to the widespread belief that forest protection is a requisite of water-resource management.

Summary and Conclusions

During the winters of 1950-51 and 1951-52 biweekly observations of soil freezing and snow depths were made in six areas in the Northeast ranging from central Maine to northern Pennsylvania. At each area measurements were taken on 12 to 18 land-use conditions, varying in cover from bare cultivated fields to mature sawtimber stands. Average depths of concrete frost, its percent occurrence, accumulated depth, and average snow depth were analyzed and compared. Results and conclusions are as follows:

Frost Depth

1. During the two winters, frost penetrated to depths of 3 to 7 inches in open lands and 0 to 5 inches in forest lands, averaging roughly 5.0 and 2.5 inches of frost depth, respectively.
2. Frost penetration in hardwood stands averaged about one-half that in conifer stands—1.5 inches compared to 3.0 inches.
3. At two of four study areas, frost was significantly deeper (1.2 vs. 2.8 inches) under hardwood reproduction than under hardwood poletimber and sawtimber stands.
4. At one of two study areas, grazed hardwood stands had significantly greater frost depth. Light logging had little effect on frost depth.
5. There was no consistent difference between frost depths in hardwood reproduction on abandoned lands and on recently clear-cut areas.
6. Frost depths were not significantly different under hardwood poletimber and sawtimber stands.
7. Differences between frost depths under 12- to 18- and 30- to 35-year-old conifer plantations were not significant.
8. Comparisons of frost depth in conifer plantations, conifer poletimber, and conifer sawtimber stands revealed no consistent differences.

Frost Occurrence

9. Concrete frost was observed over twice as often in open land as in forest lands, averaging 72 and 31 percent of observations, respectively.
10. Frost occurred twice as often in conifer stands as in hardwood stands, averaging 40 percent and 20 percent.
11. On open-land plots, frost was observed at all 4 points of measurement 73 percent of the time and at 1 of 4 points 86 percent of the time. Comparable percentages for conifer and hardwood conditions were 46 vs. 70 percent and 23 vs. 41 percent.
12. Frost occurrence has a highly significant correlation with frost depth (0.876). For each increase of 1 inch in frost depth, the percentage of observations in which frost was observed increased 13 percent.

Accumulated Depth

13. Mean frost accumulation in inch-days in the forest was about one-sixth that in the open: 74 inch-days compared to 412 inch-days.
14. Conifer values for frost accumulation compared to hardwood gave about an 8 to 1 ratio: 136 inch-days to 16 inch-days.
15. Based on accumulated depth, three distinct categories of frost intensity were classified: *high*, for open-land conditions; *intermediate*, for brushy land and conifer stands; and *low*, for hardwood cover.
16. Frost intensity in open lands was 4 times greater than in brush lands and conifer sites and 23 times greater than in hardwood stands.

Snow Depth

17. Snow accumulated to greater depth in the forest than in the open, averaging respectively, for all areas, 8.0 and 4.1 inches.
18. On an average, snow depths were about 2.7 inches more in hardwood stands than in conifer stands.
19. Hardwood forest and reproduction conditions had on an average 1.75 times deeper snow than was measured in the open; snow depths were 1.5 times greater in conifer forests than in open land.

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Oviposition Behavior of the Swaine Jack-Pine Sawfly

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LARVAE of the Swaine jack-pine sawfly (*Neodiprion swainei* Midd.) feed on the mature foliage of jack-pine (*Pinus banksiana* Lamb.). Larval development is completed by late summer, and the species overwinters in the cocoon. Adults eclose during the late spring or early summer of the following year, and after mating, the females lay their eggs in clusters in a characteristic pattern that has been described and illustrated by Atwood (1938) and by Atwood and Peck (1943). Atwood (1938) describes the oviposition pattern as follows:

> "Adult sawflies emerge from the cocoons in late June or early July. At this time the young needles of the jack pine are about one inch long and the two needles which grow from each sheath are still close together for their whole length. The slits for the reception of eggs are made in such a way that each pair of needles bears a pair of eggs placed opposite each other."

Again in 1943 a similar description is given:

> "The eggs are laid in pairs, one in each of the two needles that arise from a common base. The eggs are generally so spaced that each member of the pair occupies the same relative position on the needle."

It was this descriptive work, which called attention to the peculiar pattern of the egg scars of this species, that prompted the present study. One may read into these descriptions the implication that the insect reponds to the paired nature of jack-pine needles. In the first description, the stress placed on the proximity of the paired young needles over their entire length suggests that the insect straddles both needles at once, and transfers its attentions from the first to the second needle without appreciable movement. Such a behaviorism would certainly place a pair of eggs opposite each other on adjacent needles, but it would also call for a complex system of alternatively blocked and released responses to permit the insect to move on after laying every second egg. One might postulate, of course, that the insect retains some memory of the spa-

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tial relations of egg and needle as it moves from one needle of the pair to the other, but a performance of this complexity might reasonably be suspected to lie outside the realm of insect behavior.

In an earlier paper, Ghent (1955) reported that adults of the jack-pine sawfly (*N. pratti banksianae* Roh.) failed to provide any positive evidence that they were cognizant of the paired nature of jack-pine needles. The jack-pine sawfly lays its eggs in late summer when the foliage of the current year is mature, and on this strongly divergent foliage the eggs were found on both, one, or neither needle of the pair in almost exactly the ratio predicted from the appropriate binomial calculations. In this earlier paper the oviposition behavior of *swainei* on new foliage was held to be in sharp contrast to that of *banksianae* on mature, strongly divergent foliage; and it was of course the initial belief that this contrast would be meaningful that prompted our earlier application of binomial calculations to the egg clusters of *banksianae*.

Analysis for Pairing of Eggs by N. swainei

Field collections in the summer of 1956 in the Lac Gagnon area of Quebec provided large numbers of egg clusters of N. *swainei*, and 40 of these were analyzed in a manner similar to that reported in 1955. The 40 clusters are divided into 7 groups in Table 1, ranging in egg density from approximately 1 egg-bearing needle out of 4 in the first group (p. = .241), to approximately 8 egg-bearing needles out of 10 in the seventh group (p. = .790). These "average" values of egg density in column 3 represent recalculations for each group of egg clusters considered as a continuous whole. As in the 1955 presentation for *banksianae*, the boundaries of an egg cluster

TABLE 1. Comparison of the observed incidence of the possible combinations of blank and egg-bearing needles with the expected values.[1]

No. of clusters	Ratio: egg-bearing to total needles		Needles of pair bearing eggs			Chi-square	Probability
	Range	Average	both (p^2)	one ($2pq$)	neither (q^2)		
4	.223 —.258	.241	9 (9.9)	64 (62.2)	97 (97.9)	0.21	.65
4	.304 —.325	.317	12 (14.3)	66 (61.4)	64 (66.3)	0.79	.40
9	.384 —.434	.414	87 (84.7)	235 (239.7)	172 (169.6)	0.18	.70
7	.462 —.511	.494	82 (83.0)	172 (170.0)	86 (87.0)	0.05	.85
3	.541 —.556	.552	82 (78.9)	122 (128.1)	55 (52.0)	0.58	.45
9	.584 —.651	.611	165 (160.0)	194 (204.0)	70 (65.0)	1.03	.30
4	.741 —.836	.790	102 (101.1)	52 (53.8)	8 (7.1)	0.18	.70
40							

[1]Values, in parentheses, derived from the expansion of $(p + q)^2$.

have been taken as the uppermost and lowermost needle pairs bearing eggs. In the present study, however, no correction for blank needle pairs above or below the "cluster" as defined has been made. With the data divided into such small groups of clusters, no appreciable error accumulates and this correction can be neglected.

Expected values for the number of needle pairs bearing eggs on both, one, or neither needle of the pair have been derived by multiplying the decimal fractions p^2, 2pq, and q^2 by the total number of needle pairs in the group, a figure obtained by adding the observed frequencies in columns 4 to 6. Inspection of the data in these columns will indicate that throughout the range of egg densities in these 40 clusters there is excellent agreement between the observed frequencies and those to be expected from a purely random selection of oviposition sites. It must be concluded that *N. swainei*, like *N. p. banksianae*, does not modify its egg-laying behavior in relation to the needle pairs, and like *banksianae* affords no positive evidence that it is cognizant of the paired nature of jack-pine needles.

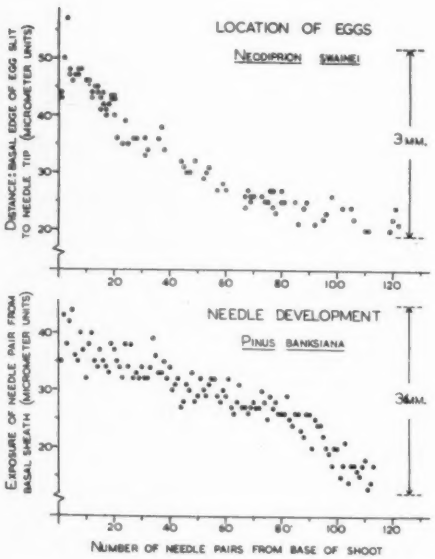
LOCATION OF EGGS
NEODIPRION SWAINEI
DISTANCE: BASAL EDGE OF EGG SLIT TO NEEDLE TIP (MICROMETER UNITS)
3MM.
NEEDLE DEVELOPMENT
PINUS BANKSIANA
EXPOSURE OF NEEDLE PAIR FROM BASAL SHEATH (MICROMETER UNITS)
3MM.
NUMBER OF NEEDLE PAIRS FROM BASE OF SHOOT

FIGURE 1. *Upper: gradient in position of egg slits of* N. swainei *on needles from the base to the tip of the shoot. Lower: similar gradient in the exposure of developing jack-pine foliage from the basal sheath, measured during the* swainei *oviposition period.*

Position of Egg-slits Relative to the Needle and to Each Other

The foregoing analysis left unanswered the problem of the positioning of eggs at the same relative height on adjacent needles of a pair when both are selected as oviposition sites. For it is true that this positioning effect is most striking: if the mature needles of a strongly divergent pair are brought together, the points at which eggs have been deposited, independently on each needle as we must now look upon it, will be found to coincide almost exactly. As a field recognition character, the occurrence of at least a portion of the eggs paired side-by-side on adjacent jack-pine needles is entirely diagnostic of oviposition by the Swaine sawfly.

For egg-cluster analysis we have adopted the convention of ordering the needles from the base to the tip of the shoot. Holding the shoot by its base, and rotating it, one is presented by the lowest remaining needle pair on the shoot after each previous pair has been tallied and removed. In handling shoots in this way while accumulating data for the binomial analysis, the impression was gained that on needles at the base of the shoot the egg slits were farther removed from the needle apices than were the egg slits on needles towards the shoot tip. Measurements of this distance from the basal edge of the egg slit to the needle tip revealed that this impression was correct, and the results of one such set of measurements are presented in the upper part of Figure 1. These measurements are given in micrometer units, but at the extreme right of the figure the spread equivalent to three mm. is indicated. This spread encompasses all but one of the 86 measurements given in the upper part of Figure 1, so that it is not surprising that this orderly regression of egg

position from the base to the tip of the shoot did not become apparent until the individual needles were handled in some systematic way.

The extreme regularity of this regression in egg-slit position satisfied the requirements of a system that could place egg slits at the same height on adjacent needles of a pair when both were selected for oviposition. The appearance of this regression led to the hypothesis that there might be a similar gradient in exposure of the developing needles from the basal sheath during the spring, and that the insect might be locating its egg slits with reference to the basal sheath. If a gradient in needle exposure existed, oviposition either as close as possible to the basal sheath, or at some fixed distance from its apical edge, would in either case produce the effect illustrated in the upper part of Figure 1. Observations and measurements made during the spring of 1957 confirm that such a gradient in needle exposure on the new shoots does occur, and one such set of measurements is presented in the lower part of Figure 1. The shoot represented by these measurements was collected at Ste. Marie on June 19, 1957, at a time when the shoot itself was approximately 7 inches in length, and the individual needles, including the basal sheath, ranged from 11 mm. in length at the base of the shoot, to 7 mm. at the tip. It can be appreciated from this figure that the range in needle exposure, again about 3 mm., is exactly that required to encompass the range in egg-slit positioning earlier observed.

Finally in this connection we have now observed, under both field and laboratory conditions, that female *N. swainei* cut their egg slits as close as possible to the basal sheath. In some instances the fresh egg slit appears actually to have been cut *through* the filmy apex of the basal sheath, though this does not seem to be an invariable rule. Figure 2 illustrates the appearance of an egg slit photographed within a few hours of its being cut. Approximately 5 mm. of needle tissue were exposed from the basal sheath at this time. Pine foliage elongates by growth at the basal end, so

FIGURE 2. *Pair of jack-pine needles developed to a total length of approximately 10 mm. Arrow indicates position of a single egg slit on the left-hand needle, just above the basal sheath.*

that had this needle pair been allowed to complete its growth, the distance between the egg slit and the needle tip would have remained the same and would have preserved a record of the length of needle exposed from the basal sheath at the time of oviposition. Observation of ovipositing females caged on branch tips of small trees near Sault Ste. Marie, Ontario, indicated that although a few prolonged their egg laying a week or more, the majority completed oviposition in less than 2 days. Little needle elongation takes place in this short time, so that in effect the ovipositing female is drawing a line with its egg slits along the top of the basal sheaths and leaving a "date stamp" on the needles as a record of the extent of their development at the time of oviposition. Thus we can determine from examination of the egg clusters that *swainei* oviposition is largely completed before the needles are exposed by more than half an inch.

The side-by-side position on adjacent needles, still recommended as an entirely diagnostic feature of *swainei* egg clusters, is now seen to be the result of the chance selection for oviposition of both needles of a pair arising from a common basal sheath. Ovipositing females on caged branch tips were observed to wander over the shoot for 2 to 3 minute intervals, or longer, between cutting successive egg slits. During these periods on needles that were then abandoned the females often adopted the oviposition orientation facing the needle tips, going through the initial probing movements as if about to cut an egg slit. The needle finally adopted for the next egg slit was often widely separated from the needle previously used.

In Figure 2 the apex of the basal sheath appears lacerated just below the egg slit, a tearing that may indicate oviposition through the basal sheath, or may have been produced by the growth and expansion of the needle pair. The position at the apex of the basal sheath may be selected either for the greater purchase that is perhaps provided to the tip of the ovipositor by this filmy tissue, or for the rigid support given by the sheath to the young needles at this point. In either case the basal sheath serves as a common reference point for a first egg slit cut on one needle; for a second egg slit cut on the adjacent needle should the same needle pair be selected by chance a second time; and even, as sometimes happens, for additional egg slits cut on the opposite edges of the needles. Several of the egg clusters examined in this study appeared to have received two or more distinct series of egg slits, each distinguished by a characteristic displacement from the needle tips. The distance between these separate series of egg slits must represent needle growth between periods of oviposition. Oviposition by a single female, spread over a week to 10 days at the most rapid period of needle elongation, or by several females utilizing the same shoot in succession, might be expected in either case to produce egg clusters of this appearance.

The observation of a gradient in needle exposure from the basal sheath during the period of needle elongation was new to the present authors, although it is apparently known to workers in more strictly botanical disciplines. Turner (1956) has recorded the same pattern of needle elongation in *Pinus ponderosa* Laws. in northern Idaho, describing the pattern as a wave of growth progressing from the base of the needle producing zone to its apex, so that "each needle in turn commences growth slightly earlier than the one above." Observations on the shoot growth of white pine (*P. strobus* L.), red pine (*P. resinosa* Ait.) and Scotch pine (*P. sylvestris* L.) near Sault Ste. Marie have confirmed that these species share this same pattern of needle elongation, so that this may perhaps be assumed to be characteristic of the shoot growth of pines.

Additional Analyses

Data gathered were interpreted, so far as possible, in relation to the earlier study of *banksianae*. There seems to be no opportunity for *swainei* to express the more striking of the behaviorisms disclosed by the

study of *banksianae* egg clusters. Laying only one egg per needle, *swainei* affords no comparison with the tendency of *banksianae* to vary its egg number per needle with the needle length. Moreover, *swainei* lays a similar total egg number, from 70 to 110 eggs per cluster, so that in laying these singly *swanei* tends to spread its egg cluster over the entire shoot, in contrast to the strong tendency of *banksianae* to concentrate its oviposition on needles towards the shoot apex.

The 1955 study of *banksianae* reported nearly 2½ times more basal than apical needle edges selected for oviposition. This feature was then related to the selection in a ratio of about 6 : 1 of lower as against upper needle edges in a gravitational sense, the predominant orientation of jack-pine shoots at angles above the horizontal placing a majority of the basal edges in the position of being the gravitational lower edge. In *swainei* egg clusters basal edge laying was found to predominate to an even greater degree: of 561 egg-bearing needles on 13 clusters, 526 bore their eggs on the basal edge, giving a ratio of almost exactly 15 : 1.

Inspection of new shoot growth at the time of *swainei* oviposition in the spring of 1957 indicated that the apical edges, lying closely against the shoot and against the needles above, are in most instances inaccessible to an insect as large as an adult sawfly. The gravitational relations of the needle edges appear, therefore, to have little bearing on the extreme predominance of basal edge laying in this instance. This conclusion was borne out by the observation of a relatively much higher incidence of apical-edge laying on the circlet of apical edges exposed near the terminal bud. Adopting the tenth needle basal to the terminal bud as a conventional boundary for this group of needles, basal-edge laying was found to predominate within this group in a ratio of only 58 : 20, or approximately 3 : 1. Over the remainder of the shoot, basal-edge laying predominated in a ratio of 468 : 15, or about 31 : 1. Re-grouping the data, the original ratio of 526 : 35 or 15 : 1 is again obtained, but this ratio obscures the fact that apical-edge laying is not an equi-probable event at all points on the snoot.

Discussion

Detailed studies of animal behavior are of value for their own sake, but on occasion they may suggest phylogenetic relations and pathways of speciation more dramatically than the morphology of the animals. Ross (1955) has pointed out that *swainei* belongs to a complex of four closely related species: *pini-rigidae* (Norton), *excitans* Roh., a new species *hetricki* Ross, and *swainei* itself. Hetrick (1956), in a report on the life histories of five *Neodiprion* sawflies, describes the oviposition behavior of *hetricki* as follows:

> "There is a single generation each year with adults depositing overwintering eggs in October. A female of the species lays only one egg to a needle, but a single pine terminal may contain approximately a hundred eggs. *The site of the single egg per needle is just above the needle sheath.* By the following spring each egg is surrounded by a halo of dead needle tissue and the position of the eggs may be seen by the casual observer."

The portion of this quotation that we have placed in italics suggests a close relation between the behavior of *hetricki,* and the behavior of *swainei* as disclosed by the present study. Oviposition and larval feeding by *hetricki* take place on the mature, 6- to 9-inch needles of loblolly pine, *P. taeda* L. On these very long needles, *hetricki* oviposits in exactly the same position used by *swainei* on needles that may be exposed from the basal sheath by only a few millimeters. It is possible that *pini-rigidae* also lays its eggs against the basal sheath, for an old description by Packard (1890) states that "the female lays her eggs singly in one side of a needle of the pine, though sometimes an egg is inserted on each side of the leaf." No more recent references have been found for the oviposition be-

havior of this species, while the behavior of *excitans* seems not to have been described at all.

The laying of a single egg through or against the basal sheath is a behavior pattern distinct from that of the majority of pine sawflies that arrange their egg slits in a row along the needle edge. At our present level of knowledge such a single-egg pattern seems to make adaptive sense only for *swainei*, for in this instance it allows utilization of needles as oviposition sites when as little as one or two mm. of needle tip are exposed. Moreover, it permits considerable leeway in phenological synchrony during the period of needle elongation: oviposition may proceed on the new needles at any time after they have broken from the basal sheath. This latter contention is supported by the wide range in the position of *swainei* eggs that can be found in the mature foliage of the current year. Among the clusters examined were a few on which the eggs had been laid at a point nearly ¾ of an inch from the needle tip, but again showing the minute gradient in position indicative of oviposition at the basal sheath. Presumably then the entire period of needle elongation is available for oviposition by this species.

The same behavior, when displayed by *hetricki* on the mature foliage of loblolly pine (*Pinus taeda* L.), would appear to be entirely bizarre unless one assumes that *hetricki* arose from an ancestor having the *swainei* pattern of developmental chronology and oviposition. The opportunity for such speciation may well have been provided during a glacial period in which the ranges of the respective host trees were compressed in southern North America. It is unlikely that a southern pine such as *P. taeda* would have been available for exploitation by a *swainei*-like ancestor without a change in the developmental chronology of the insect. In the cooler climate that would then have prevailed, the northern invaders, both host and insect, would be well adapted to early spring development, while more southerly species might be expected to lag behind. Under these circumstances speciation might well have proceeded through the selection of a population that completed pupal development without overwintering, and was then capable of laying on mature foliage. The raw material for such selection seems even today to be present in *swainei* populations, for under laboratory conditions at least, occasional *swainei* adults eclose in the fall without overwintering as cocooned prepupal larvae. We have no recorded observations of *swainei* overwintering in the egg stage, though one might now predict that if such occurs the eggs will be found at the base of the mature needles, close against the basal sheath.

It is not within the scope of this paper to review the extensive literature on the analysis of pollen from unglaciated bogs in the United States, though much of it is pertinent to the problem of the distribution of tree species during glacial times. Fortunately such a review has recently been provided by Braun (1955), and from the bibliography in this review the papers of J. E. Potzger and of D. G. Frey are especially noteworthy. The weight of contemporary opinion in this field seems to support the contention that during recent periods of glacial advance a pine species, having pollen grains of the small size characteristic of present-day jack pine, occurred as a widely distributed intrusive from the boreal forest well into the range of loblolly and other southeastern pines.

It may become profitable to examine another possible pathway of evolution between *swainei* and *hetricki* when we have at least an elementary knowledge of the biology of *exitans* and *pini-rigidae*. It is possible that *pini-rigidae* might emerge as the present-day representative of an ancestral bridge between *swainei* and *hetricki*, since *pini-rigidae* has as its host a tree species—pitch pine (*Pinus rigida* Mill.)—that is closely allied to jack pine and that provides even in its present distribution a bridge between the distributions of jack and loblolly pines. In the same way the remain-

ing sawfly in this group, *exitans*, may emerge as the representative of a further bridge between *pini-rigidae* and *hetricki*. Ross (1955) records *Pinus echinata*, *P. taeda*, and *P. rigida serotina*[1] as the known hosts of *exitans*. The pond pine (*P. serotina* or *P. rigida serotina*) appears to have developed from pitch pine as a southern species or subspecies, and as such it probably presented few problems of adaptation to an ancestral line already adapted to *P. rigida*. One may postulate then a possible avenue of speciation and southern extension of the group as follows: a *swainei*-like ancestral line moving first to *P. rigida* and leaving the sawfly *pini-ridigae* as the present-day representative of adaptations acquired in the movement from ancestral jack pine to ancestral pitch pine; a further movement to *P. serotina* leaving *exitans* as its representative: and from this line, by then well adapted to southern climatic conditions, the final speciation to *hetricki* with a host, *P. taeda*, to which *exitans* is also adapted. Study of the biology of *exitans* and *pini-rigidae* offers as an immediate reward the opportunity to clarify the point at which egg-stage overwintering, as exemplified by *hetricki*, might have emerged along this postulated evolutionary pathway. It is possible that it was this change in overwintering habit that separated *hetricki* from the *exitans* ancestral line that still shares *P. taeda* as one of its hosts.

This latter mechanism of speciation, that of a change in overwintering from the prepupal to the egg stage or the reverse, may possibly have acted many times in other insect groups, and may even have acted more than once in the evolution of the *swainei-hetricki* group. The change in overwintering habit effects temporal isolation of breeding adults with complete efficiency, and as a pathway of speciation it calls more urgently for a premise of geographical continuity than for one of geographical isolation. That is not to say that changes in host range, or adaptive values attributable to one pattern or the other, may not later effect a geographic separation, but only after the fact of speciation itself.

[1]The eighth edition (1950) of Gray's Manual of Botany accords full specific status to *P. serotina*, while drawing attention still to its close alliance with *P. rigida*.

Editor's note:—The Check List of Native and Naturalized Trees of the United States, Agric. Handbook No. 41, Forest Service, U. S. Dept. Agric. 1953, also lists pond pine (*P. serotina* Michx.) as a species.

Summary

Neodiprion swainei had been described as laying its eggs in pairs. The appropriate binomial calculations satisfied the observed distribution of eggs on both, one, or neither of the pair of jack-pine needles that arise from a common base, so that the existence of a *pairing* behaviorism cannot be supported. A gradient in egg position was discovered, such that the distance from egg slit to needle tip is greater on needles near the base of the shoot, and declines steadily towards the shoot tip. This gradient was related to a similar gradient in the exposure of the developing needles from the basal sheath during the spring growing season. Oviposition takes place as close as possible to the apical edge of the basal sheath, subsequent growth of the needle carrying the egg slit away from the basal sheath and preserving the original distance between egg slit and needle tip. The behavior of this species is therefore essentially the same as that of *N. hetricki*, which lays a single egg as close as possible to the basal sheath of the mature, 6- to 9-inch foliage of loblolly pine. Possible avenues of speciation that may link these species are discussed.

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